

ON CERTAIN TRIASSIC AND LIASSIC REPRESENTATIVES OF THE FAMILY PHOLIDOPHORIDAE S. STR.

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SYNOPSIS

This paper is a revision, based mainly on the exoskeleton of the head and trunk, of a number of Upper Triassic and Liassic species formerly included in the genus *Pholidophorus* Agassiz. Special attention is paid to the shape of the preoperculum, the preopercular sensory canal and the squamation. Four species of *Pholidophorus*, including the type species, *Ph. bechei*, are redescribed. In the genus *Pholidophoroides* Woodward two species are redescribed. A new genus *Pholidophoropsis* is made for *Pholidophorus caudalis* Woodward and *Pholidophoropsis maculata* sp. nov. is described. A new genus and species, *Pholidolepis dorsetensis*, is made for part of the material previously included in *Ph. caudalis*. Relationships between the various species and genera of Pholidophoridae s. str., and between the Pholidophoridae and the Parasemionotidae and Leptolepidae are discussed.

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I. INTRODUCTION

THE fundamental requisite for any discussion regarding the origin of the teleostean fishes is a knowledge of the species belonging to the family Pholidophoridae. Because of the vague definition of the genus *Pholidophorus* Agassiz 1832 many varied species have been attributed to it with the result that it has become one of the most extensive holostean genera, obviously containing many heterogeneous elements of dubious affinity. Consequently a revision of the genus *Pholidophorus* has long been highly desirable.

In 1941 Woodward took up the question. Besides the genus *Pholidophorus* s. str., with *Ph. bechei* Agassiz as type species, he created three new genera : *Pholidophoroides* with *Ph. crenulatus* Egerton as type species and with *Ph. caudalis* Woodward as probably belonging to the same genus, *Pholidophoristion* with *Ph. ovatus* Agassiz as type species and *Ph. micronyx* Agassiz as second member, and *Ichthyokentema* for the two species *Ph. purbeckensis* Davies and *Ph. brevis* Davies. The last named genus has recently been treated in an excellent manner by Griffith & Patterson (1963), and its differences from *Pholidophorus* have proved to be so striking that a new family, Ichthyokentemidae, has been erected for it. The genera *Pholidophoroides* and *Pholidophoristion* have, however, not yet been thoroughly investigated and their validity consequently not proved.

A rather large number of specimens referred to the species *Ph. caudalis* Woodward and belonging to the British Museum (Natural History) attracted my attention because some of them showed a striking similarity to members of the genus *Leptolepis*. Because of this I have tried to study this material in more detail and have arrived at the conclusion that the specimens labelled as *Ph. caudalis* represent numerous different species. As *Ph. caudalis* was considered by Woodward as probably belonging to his new genus *Pholidophoroides* I have also found it necessary to take the type species *Ph. crenulatus* into consideration, and have tried to make a redescription of this species based on the excellent material in the British Museum (Natural History). From Woodward's (1895) description of *Pholidophorus limbatus* Agassiz it seemed to me not unlikely that the species could have some relationship to the genus *Pholidophoroides*. It is therefore included here.

A definition of the genus *Pholidophoroides* required a comparison with the type species of the genus *Pholidophorus*. It is, however, not obvious which species should be considered as the type species of this genus. The genus *Pholidophorus* was erected by Agassiz (1832) for the two species *Ph. latiusculus* and *Ph. pusillus* from the Upper Trias of Seefeld, Tyrol. The diagnoses for the genus and for the two species are rather scanty and meaningless : "*Pholidophorus* Ag. Häringsgestalt. Grosse rautenförmige Schuppen. Schwanzflosse ziemlich gleichlappig, indessen ziehen sich die Schuppen noch an den obern Lappen hinauf. Rückenflosse den Bauchflossen gegenüber. Afterflosse sehr klein.

"1. Ph. latiusculus Ag. Grössere Schuppen. Im Verhältniss breiter als der folgende.

"2. Ph. pusillus Ag. Beide von Seefeld in Tyrol. In der Sammlung meines Freundes Dr. Alex. Braun, und letztere auch im Museum in Carlsruhe." In his later work Agassiz (1833, 2:9) mentions the genus *Pholidophorus* for the first time, with the following five species :

"1. *Pholidophorus limbatus* Agass. Ecailles frangées à leur bord postérieur. Corps très-allongé. Lias : Lyme Regis.

"2. Pholidophorus dorsalis Agass. Caractérisé par de longs chevrons sur le bord du premier rayon de la dorsale. Lias : Seefeld.

"3. Pholidophorus latiusculus Agass. Plus court ; écailles plus grandes. See-feld.

"4. Pholidophorus pusillus Agass. Ecailles très-petites. Seefeld.

"5. *Pholidophorus microps* Agass. Tête petite ; écailles en scie fine à leur bord postérieur, plus hautes que larges. Sohlenhofen."

A more exhaustive description of the genus and its twenty species follows on p. 271 of the same volume (1844); the first one treated is *Ph. bechei* Agassiz. *Ph. latiusculus* is only mentioned on p. 287 as the second species (after *Ph. dorsalis*) among those which were not figured for want of space but which the author intended to describe later on. The short note on *Ph. latiusculus* runs as follows: "Du lias de Seefeld et de Lyme Regis. Espèce très-voisine de la précédente, mais plus petite, ayant la dorsale moins reculée; elle n'a guère que deux à trois pouces de long."

The first species ascribed to the genus *Pholidophorus* is thus *Ph. latiusculus*, but Agassiz never named a type species of the genus nor a holotype of *latiusculus*, and never gave a figure of it; the diagnoses cited above are too meagre and meaningless to allow an exact identification of the species. In his treatment of the fossil fishes from the Upper Trias of Seefeld, Kner (1866) tried to identify the three *Pholidophorus* species *dorsalis*, *latiusculus*, and *pusillus*, but says regarding the proposed identification: "Ich hoffe hiedurch wenigstens anderen Paläontologen festere Anhaltspunkte zur Unterscheidung der Arten zu bieten und ihnen anschaulich zu machen, welche Formen mindestens mir den drei Arten von Agassiz zu entsprechen scheinen; ob meine Deutung die richtige sei, darüber mögen sie selbst dann entscheiden." Woodward (1895) obviously accepted the identification proposed by Kner and I cannot find any objection to this.

Regarding the type species of the genus *Pholidophorus* Woodward did not choose the first named *latiusculus* but *bechei*, the first species described and figured by Agassiz (1837, 2, pl. 39, figs. I-4; 1844, 2:272). Woodward (1895:450-451) gives a good diagnosis of the latter species, which has more recently been investigated by Miss Rayner (1941, 1948), who was, however, principally interested in the study of the endocranium; her description of the exoskeletal cranial bones and the accompanying text-figures are thus rather schematic and do not allow a detailed comparison with other, closely related species. Consequently I have found it necessary to attempt a redescription and a new reconstruction of the exoskeletal cranial bones, based on some specimens belonging to the Department of Palaeontology, British Museum (Natural History).

The descriptions of *Ph. latiusculus* given by Kner (1866) and Woodward (1895) are also quite insufficient today. During a visit to Innsbruck in November 1963 I had

the opportunity to see in the Univ.-Institut für Geologie und Paläontologie some specimens from Seefeld, identified as *Ph. latiusculus*, among them a rather well preserved specimen figured by Kner (1866, pl. 3, fig. 3). As *Ph. latiusculus* seems to be closely related to *Ph. bechei* I find it convenient to append a short description of this species also, partly based on the specimens loaned from Innsbruck, partly on specimens belonging to the British Museum (Natural History), as well as of another interesting species, *Pholidophorus caffii* Airaghi, the holotype of which has been kindly placed at my disposal by the Director of the Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy. The description of a specimen probably belonging to *Pholidophorus pusillus* has also been included.

Unless otherwise stated all the registered numbers given in the text refer to specimens in the British Museum (Natural History) collections.

II. SYSTEMATIC DESCRIPTIONS

Genus PHOLIDOPHORUS Agassiz

1832 Pholidophorus Agassiz : 145.

PRELIMINARY DIAGNOSIS. Pholidophoridae of small to medium size. Exoskeletal cranial bones and scales with ganoin covering. Nasal well developed and well separated from its antimere by the frontals. Two well-developed supraorbitals. Maxillary not markedly stout and deep, posterior margin evenly rounded. Two supramaxillaries, overlapping dorsal margin of maxillary ; supramaxillary 2 without a marked process at antero-dorsal corner. Antorbital rather small ; five infra-orbitals. Preoperculum with preopercular sensory canal running nearer to anterior than to posterior margin. Lower jaw not markedly deep, its greatest depth being in the posterior third of its length ; dentary with a smooth dental part, separated from ornamented splenial part by strong ridge. Dorsal fin above base of ventral fins. Fulcra present along anterior margin of at least dorsal, pectoral and ventral fins ; caudal fin hemi-heterocercal with dorsal and ventral margins fulcrated. Scales rather thick with articulating pegs and with their posterior margin smooth ; anterior lateral line scales much deeper than broad.

Type species. Pholidophorus bechei Agassiz.

REMARKS. The diagnosis given above for the genus *Pholidophorus sensu stricto* must at present be regarded as a preliminary one, and this mainly for two reasons. Firstly, it is based on two species only, the type species of the genus and *Ph. latiusculus* Agassiz; only after a thorough study of the remaining species earlier ascribed to *Pholidophorus* or at least of a good number of them, can the limits of this genus be made out and the common features of all its known species be established. Secondly, the present investigation only deals with external features, mainly the exoskeletal cranial bones; an investigation of the endocranium and the visceral skeleton will undoubtedly reveal further characteristics of value for a definitive diagnosis.

Pholidophorus bechei Agassiz

(Pls. 1, 2, 3; Text-figs. 1, 2)

1837 Pholidophorus bechei Agassiz, 2, pl. 39, figs. 1-4.

1837 Pholidophorus onychius Agassiz, 2, pl. 39, figs. 5-7.

1844 Pholidophorus bechei Agassiz, 2, 1:272.

1844 Pholidophorus onychius Agassiz, 2, 1:274.

1895 Pholidophorus bechei Agassiz; Woodward: 450, pl. 12, figs. 1, 2.

1941 Pholidophorus Rayner : 230, text-fig. 10.

1948 Pholidophorus bechei Agassiz; Rayner: 318, pl. 21, fig. 45, text-figs. 24-29.

1963 Pholidophorus bechei Agassiz; Griffith & Patterson: 31.

PRELIMINARY DIAGNOSIS. *Pholidophorus* of medium size, up to about 200 mm. in total length. Nasal very large, anteriorly rounded and reaching beyond the anterior tip of the frontal. Posterior margin of preoperculum deeply notched. Preopercular sensory canal with about 17–19 tubules.

HOLOTYPE. The first known specimen of this species is the one described and figured by de la Beche (1822) who, however, did not propose a scientific name for it ; according to Agassiz (1844, Vol. 2, pt. I : 273) this specimen was preserved in the collection of the Geological Society, London, but the specimen could not be found (March, 1965) in the collection of the Geological Survey Museum, London, where the British part of the Geological Society's collection is now housed. The specimen figured by Agassiz (1837, pl. 39, fig. 1) belonged at that time to Miss Philpot, Lyme Regis.

MATERIAL. The specimens used for the following description are Nos. 25276, 38107, 38109, 39859, P.154, P.1051, P.1052*d*, P.3586*c*, and P.3589*a*, all belonging to the British Museum (Natural History), London. Unfortunately they are all more or less defective, especially in the ethmoidal region.

DESCRIPTION. This species may attain a total length of about 200 mm. according to Woodward (1895: 450), who also states that the length of the head with opercular apparatus is somewhat less than the maximum depth of the trunk and occupies one-fifth of the total length of the fish. As the main purpose of my investigation is to study the exoskeletal cranial bones of the type species of *Pholidophorus*, I have not examined the whole material in the British Museum (Natural History) but only some specimens showing these details. The largest of them, 25276, has a total length of about 164 mm., a standard length of about 140 mm. and a length of the head of about 37 mm., thus somewhat more than one-fifth of the total length (ca. 22.5%) and about one quarter of the standard length (ca. 26%). These values correspond rather well with those given by Woodward. Of the other larger specimens P.1051 is defective but seems to be a little larger than 25276, while P.1052d is a little smaller than that specimen. 38107 and 38109 have a standard length of 113 mm. and about 125 mm. respectively. The remaining three specimens are, however, much smaller with a standard length of about 80 mm. (P.3589a), 76 mm. (P.154), and 64 mm. (39859), respectively.

Regarding the exoskeletal cranial bones no differences of taxonomic value can be observed between the larger and the smaller specimens, as far as their preservation allows a comparison. There exists, however, a marked difference regarding the development of the ganoin layer on the cranial bones as well as on the scales. In the largest specimens (Pl. 2, fig. 3) there is a continuous, thick layer of ganoin, more or less richly ornamented, on all exposed parts of the exoskeletal cranial bones and all the scales are thick. In the smaller specimens (64–80 mm. standard length; Pl. 2, figs. 1, 2) the ganoin covering is much thinner, on the exoskeletal cranial bones appearing as streaks, spots or small tuberculations, and the ganoin covering on the body scales seems to be remarkably thin in the anterior part of the body, gradually becoming thicker posteriorly. Even in 38107 (standard length 113 mm.) the scales on the anterior part of the body look thinner than in the posterior part. Perhaps this may be an indication of the beginning of the reduction of the ganoin covering which must have taken place in the phylogenetic development from the holostean to the teleostean stages of evolution.



FIG. 1. Pholidophorus bechei Agassiz. Attempted restoration of head in lateral view. \times 3.3. Ang, angular; Ant, antorbital; De. Spl, dentary; Dpt, dermopterotic; Dsph, dermosphenotic; Ext, extrascapular; Fr, frontal; Ifo₁-Ifo₅, infraorbitals I to 5; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pa, parietal; Pmx, premaxillary; Pop, preoperculum; Ro, rostral; Sbo, suborbital; Smx₁, Smx₂, anterior and posterior supramaxillaries; So₁, So₂, anterior and posterior supraorbitals; Sop, suboperculum; Ssc, suprascapula; ap, anterior pit-line; hc₁, anterior division of supramaxillary pit-line; ifc, infraorbital sensory canal; ifc. com, ethmoidal commissure; mp, middle pit-line; orp, postmaxillary pit-line; orp₁, oral pit-line; poc, preopercular sensory canal; s. com, supratemporal commissure; soc, supraorbital sensory canal.

Exoskeletal skull roof

The *premaxillary* (*Pmx*, Pl. 1; Pl. 2, figs. 1, 2; Pl. 3, figs. 3, 4; Text-fig. 1) has the form of an equilateral triangle with the dorsal margin almost straight, the posterodorsal margin weakly S-shaped to fit the margin of the maxillary, and the anteroventral margin a little convex and carrying a single row of 15 or more curved teeth. The slightly bulging outer surface carries a few ganoin tuberculations.

The rostral (Ro, Pl. 2, figs. 2, 3; Text-figs. 1, 2) is best preserved in the small specimen P.3589*a*. Its median, bulging part is ornamented with a few ganoin spots, its ventro-lateral parts are, however, very defective and nothing can be made out with accuracy regarding the outline of the bone. In P.1052*d* parts of the rostral can also be observed.

The nasal (Na, Pl. 2, figs. I-3; Text-figs. I, 2) is comparatively very large. Anteriorly it is evenly rounded; in its posterior part it tapers gradually backwards. In the smallest specimen investigated, 39859, its lateral margin has an almost semicircular notch for the posterior nasal opening (Pl. 2, fig. I), in the largest specimen P.I052d, this opening is entirely surrounded by the bone (Pl. 2, fig. 2) just as figured by Miss Rayner (1941, text-fig. IO). In these two specimens as well as in P.3589a the nasals of both sides are well separated by the anterior tip of the frontals; nothing indicates that the nasals meet in the mid-line as figured by Miss Rayner. In the smallest specimen the dorsal surface of the nasal is quite smooth but in the two other specimens mentioned it is provided with a few ganoin spots, principally on the ridge indicating the course of the supraorbital sensory canal.

The frontal (Fr, Pl. 2, figs. I-3; Text-figs. I, 2) is pointed in its anterior part, mesial to the nasal, and from this region backwards it becomes progressively broader and has its broadest part posteriorly. Above the orbit the frontal margin is slightly concave, posterior to it the margin is almost straight and posteriorly directed. The postero-lateral corner of the frontal is rounded off and its posterior margin seems to be slightly wavy. The suture between the frontals of both sides is straight anteriorly but in the middle of its course it is irregularly sinuous, its path varying from specimen to specimen. The dorsal surface of the frontal is practically smooth in the smallest specimen (Pl. 2, fig. I); in P.3589*a* there are smaller and larger, partly confluent ganoin spots (Pl. 2, fig. 2) and in the large specimen, P.1052*d*, the whole dorsal surface of the frontal is covered with ganoin forming radiating ridges of tuberculations on the lateral part of the anterior half of the bone (Pl. 2, fig. 3).

There are two well-developed supraorbitals. The anterior one, supraorbital I (So₁, Pl. 2, figs. I-3; Text-figs. I, 2), is situated in the angle between nasal and frontal; its posterior half is rather broad and posteriorly rounded off, anterolaterally it tapers considerably. In the smallest specimen, 39859, its surface is smooth, in P.3589*a* and especially in the large specimen, P.IO52*d*, the surface is ornamented with ganoin tuberculations. Posterior to supraorbital I there is an elongate supraorbital 2 in P.3589*a* (So₂, Pl. 2, fig. 3; Text-figs. I, 2); its mesial margin is slightly convex, fitting the concave margin of the frontal, anteriorly it tapers gradually. Its dorso-lateral surface is covered with a rather thick ganoin



FIG. 2. Pholidophorus bechei Agassiz. Attempted restoration of head in dorsal view. \times 3.3. Lettering as in Fig. 1.

layer. In P.1052*d* there is posterior to supraorbital 1 a small, rounded supraorbital 2; it seems not to be broken off posteriorly; some bone fragments posterior to it may be other parts of the same bone, perhaps fragmented during an early stage in the ontogenetic development (So, Pl. 2, fig. 2).

The *dermosphenotic* (*Dsph*, Pl. 1; Pl. 2, fig. 2; Text-figs. 1, 2) is missing in most specimens, and in P.1052*d* only fragments of it are visible. In 38107, however, a rather well-preserved, roughly triangular dermosphenotic is present with its dorso-posterior margin convex and with its slightly concave and thickened anterior margin constituting the postero-dorsal border of the orbit.

The shape of the exposed surface of the *parietal* (Pa, Text-figs. 1, 2) is difficult to determine because of the poor preservation of this part of the skull roof, but it seems to be roughly square.

The *dermopterotic* (Dpt, Pl. 2, figs. 1-3; Text-figs. 1, 2) is comparatively narrow in its anterior part lateral to the posterior part of the frontal, but it broadens posterior to that bone on the dorsal surface of the skull, where it meets the parietal.

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The extrascapular (Ext, Pl. 1; Pl. 2, fig. 2; Text-figs. 1, 2) is heavily crushed in all specimens investigated by me, but it seems to have the usual triangular shape.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pl. 1; Pl 2, figs. 1, 2; Pl. 3, figs. 3, 4; Text-fig. 1) is anteriorly pointed but it deepens ventrally, posterior to the premaxillary, so that a notch is formed for the premaxillary. The maxillary then becomes deeper with its greatest depth near its evenly rounded posterior margin ; its ventral margin is evenly convex. The dorsal margin, on the whole slightly concave, is overlapped by infraorbital I (lachrymal) and the two supramaxillaries; anteriorly, at the deepening of the maxillary, its dorsal margin shows a shallow but marked concavity for the anteroventral part of infraorbital I. The lateral surface of the maxillary is ornamented with a longitudinal striation which is parallel to the dorsal and ventral margins in the larger specimens; however, in the smallest specimen, 39859, this ornamentation is only feebly marked (Pl. 2, fig. 1), in the somewhat larger specimens, P.154 and P.3589a, the ganoin streaks are broader and more irregularly arranged. Regarding the dentition along the ventral margin of the maxillary nothing can be said with accuracy because of the defective state of preservation; in 38107 and 38109 the posterior part of the ventral margin shows, however, some markings which suggest a feeble dentition, and in P.3580a the same part carries a delicate, comb-like dentition as in Leptolepis.

The two supramaxillaries $(Smx_1, Smx_2, Pl. I; Pl. 2, fig. 1; Pl. 3, fig. 4; Text$ fig. 1) are situated dorsal to the posterior part of the maxillary, partly overlappingits dorsal margin. The anterior one, supramaxillary I, is comparatively small androughly semicircular with its ventral margin straight. Its lateral surface has aganoin ornamentation of irregular patches in the smaller specimens; in the largerspecimens they are confluent. In 38109 and P.1051 the anterior tip of the bonecarries a well marked <-shaped crest parallel to its margins (Pl. 3, figs. 4, 5). Theposteriorly situated supramaxillary 2 is much larger than supramaxillary I andalmost triangular in shape with its greatest depth anteriorly; its ventral margin isstraight, its dorsal margin convex, and its anterior margin concave to fit the convexmargin of supramaxillary I. Its antero-dorsal tip is slightly produced, and isapparently more pronounced in the smaller specimens. The lateral surface ofsupramaxillary 2 is ornamented with irregular ganoin spots in the smaller specimens:in the larger ones the entire surface is covered by a layer of ganoin with feebly markedtuberculations.

The six bones of the infraorbital series (antorbital—five infraorbitals) are rather well preserved.

The antorbital (Ant, Pl. 2, fig. 1; Pl. 3, fig. 2; Text-figs. 1, 2), well exposed in 25276, 39859 and P.3586c, is comparatively small, almost triangular in shape with the angles rounded off. Its anterior and ventral margins are slightly convex and its posterior margin is straight or moderately concave.

Infraorbital I (lachrymal) (If o_1 , Pl. 2, fig. I; Pl. 3, figs. 3-5; Text-fig. I) is well preserved in 38109. It is elongate and deepest anteriorly. Its convex ventral

margin has anteriorly a shallow notch, its postero-dorsal margin is not entirely visible but seems to be slightly concave.

Infraorbital 2 (If o_2 , Pl. I; Text-fig. I), clearly visible in 38107, has the usual elongate shape with the dorsal margin slightly concave. The ventral margin is slightly convex.

Infraorbital 3 (Ifo₃, Pl. I; Pl. 2, fig. I; Text-fig. I) is by far the largest bone in the series, stretching from the orbit to the anterior margin of the preoperculum, which it slightly overlaps. Its antero-dorsal and antero-ventral margins are concave, its dorsal margin is straight and its posterior margin is slightly convex.

Infraorbitals 4 and 5 (Ifo_4 , Ifo_5 , Pl. I; Pl. 2, fig. I; Text-fig. I) are almost square with their anterior margins slightly concave and their posterior margins slightly convex. Infraorbital 5 is not entirely exposed in any of the specimens investigated but it seems to be a little smaller than infraorbital 4.

A comparatively large *suborbital* (Sbo, Pl. I; Text-fig. I) is situated posterior to infraorbitals 4 and 5 and seems to overlap the antero-dorsal part of the operculum. It is, however, generally crushed in the specimens available and in consequence of this, its outline can only be made out in part.

The *preoperculum* (*Pop*, Pl. I; Pl. 2, figs. I, 2; Pl. 3, figs. 4, 5; Text-fig. I) has a very characteristic shape. The dorsal, almost vertical limb broadens continuously ventrally. The antero-ventrally directed limb is remarkably broad. The posterior margin of the bone is deeply notched below the angle between the two limbs, the postero-ventral corner projects backwards but is rounded off, not pointed as in Miss Rayner's reconstruction, the ventral margin is almost straight or slightly convex and the anterior margin shows a rather marked convexity below the middle of the bone.

The operculum (Op, Pl. I; Pl. 2, fig. I; Text-fig. I) is roughly triangular; the straight anterior, vertical margin and the straight postero-ventral margin meet at a low angle, the dorsal margin is evenly rounded. The anterior margin seems to be a little thickened.

The *suboperculum* (Sop, Pl. I; Pl. 3, figs. 4, 5; Text-fig. I) is comparatively large, but it is not entirely preserved in any of the specimens investigated and consequently its outline cannot be made out with accuracy. The antero-dorsal process anterior to the ventral tip of the operculum is comparatively strong.

The posterior part of the *interoperculum* (*Iop*, Pl. 1; Pl. 3, figs. 4, 5; Text-fig. 1) is well exposed in 38107, 38109, and P.1051; its anterior part is not visible in any of the specimens investigated.

Branchiostegal rays and gular plate

Branchiostegal rays are exposed in 38107, 38109, and P.1051. In 38107 there are at least 12 branchiostegal rays on the right side (R. Br, Pl. 1), in P.1051 at least 13 rays may be distinguished, the six anterior ones still attached to the large ceratohyal 2 $(Ch_2, Pl. 3, fig. 5)$, which is unfenestrated but provided with a deep groove for the hyoid artery.

An elongate, anteriorly keeled, detached but not entirely exposed bone in P.3589*a* may be interpreted as the *gular plate* (Gu, Pl. 3, fig. 1). A fragment of a gular plate is probably visible also in P.154.

Lower jaw

The lower jaw is more or less exposed in most specimens; in P.1051 it is almost entirely free from overlying bones (Pl. 3, fig. 5); it is a little defective but the outline of the defective parts can be followed through the impression in the rock.

The dental and splenial parts of the *dentary* (*De. Spl*, Pl. 1; Pl. 2, figs. 1, 2; Pl. 3, figs. 4, 5; Text-fig. 1) are separated by a prominent ridge on the lateral surface of the bone; the anterior part of its dorsal margin is only gently ascending; at about the limit between the first and second third of the length of the lower jaw the dorsal margin of the dentary is abruptly thickened and ascends postero-dorsally. The boundary between the dentary and the angulo-supra-angular cannot be made out. The lateral surface of the splenial part is ornamented with thick striations and rugo-sities, whereas that of the dental part is quite smooth. In 38109 there are, as already stated by Miss Rayner (1948: 319), some delicate teeth a little distance from the anterior tip of the dentary (Pl. 3, fig. 4); as far as I can see there are seven.

The angulo-supra-angular (Ang, Pl. I; Pl. 2, fig. I; Pl. 3, figs. 4, 5) constitutes the posterior part of the lower jaw; its depth equals about one-third of the length of the jaw. The lateral surface of the angulo-supra-angular has ventrally a conspicuous ganoin ornamentation.

No true dermarticular can be seen. The *articular* (*Art*, Pl. 1; Pl. 2, fig. 1; Pl. 3, figs. 4, 5) is partly visible in 38109.

Sensory canal system of head

The sensory canal system of the head is well developed, but because of the bad state of preservation of certain bones it cannot be described in every detail; in particular the lack of a specimen with the bones of the snout in natural position makes the interpretation uncertain.

The supraorbital sensory canal (soc, Pl. 2, fig. 1; Text-figs. 1, 2) pierces the nasal, the frontal and the parietal.

The nasal part of the canal is clearly visible in 39859, P.1052d (Pl. 2, fig. 3), and P.3589a (Pl. 2, fig. 2); it runs in a gentle arch from the antero-lateral to the posteromesial margin of the bone, where it enters the frontal. In the large specimen, P.1052d, there is a single pore visible on the dorso-mesial side of the canal a little anterior to the fenestra for the nostril. In the smaller specimen, P.3589a, a corresponding pore may be traced on the dorso-lateral side of the canal; in the smallest specimen no pores can be observed.

The frontal part of the supraorbital sensory canal is very difficult to see because of the crushed state of the frontal in all specimens at my disposal. In the anterior part of the bone it runs, however, at first almost directly backwards, then it curves postero-laterally parallel to the lateral margin of the frontal and finally continues postero-mesially to the posterior margin of the bone. Pores or short tubules can only be observed in P.1052d, and there the state of preservation does not allow any certain conclusions. According to Rayner (1948) there is great variability regarding the number and position of tubules and pores in this part of the supraorbital sensory canal; my interpretation of the arrangement in P.1052d is given in Text-figs. 1, 2. On the left side where the canal can be followed practically without interruption, except for its hindmost part, I have observed only a single short, laterally directed tubule in the posterior part of the anterior straight course of the canal; at the curve there issue two somewhat longer, postero-mesially directed tubules from the mesial side of the canal and behind them two very short tubules on the same side of the canal; on the postero-mesially directed part of the canal there are five very short tubules or pores. On the right side, where the canal is more defective, the tubules and pores seem to have on the whole the same arrangement, as far as they are discernible.

The parietal part of the supraorbital sensory canal is visible on the left parietal; the canal itself is very short, apparently without tubules or pores. It continues backwards as a well-marked groove, the anterior pit-line (ap, Pl. 2, fig. 2; Text-figs. 1, 2).

The *infraorbital sensory canals* (*ifc*, Pl. 3, fig. 4; Text-figs. 1, 2) of both sides are joined anteriorly by a slightly arched ethmoidal commissure in the rostral. In P.1052*d* a short, posteriorly directed tubule can be seen on each side of the mid-line of the bone.

The small antorbital contains in its ventral half the curved anterior part of the infraorbital sensory canal. From its convex dorsal side the canal gives off a short antorbital branch, ending with a comparatively large pore; no more pores can be observed on this part of the canal except in 25276, where a pore seems to be present at the anterior angle between the canal and the antorbital branch (Pl. 3, fig. 2). According to Rayner (1941, text-fig. 10B; 1948, text-fig. 25) the antorbital branch joins the supraorbital sensory canal "to form a closed circuit around the eye". I cannot, however, share this opinion. As already mentioned above no specimen seen by me has the exoskeletal bones of the snout preserved in natural articulation, but when trying to reconstruct this part of the skull I have not been able to arrive at a solution other than that given in Text-fig. 1. Only much better preserved material regarding the mutual position of the bones in question can decide which solution is correct.

Passing into infraorbital I (lachrymal) the infraorbital sensory canal pierces this bone on the whole parallel to its convex anterior and ventral margins. Judging from 38109 (Pl. 3, fig. 4) the canal gives off from its anterior side three short, anteroventrally directed tubules and from its ventral side at least seven ventrally to posteroventrally directed tubules, the middle ones being the largest; as the bone is apparently not complete in its posteriormost part there might, consequently, exist one or more tubules in infraorbital I in addition to the ten observed by me.

In infraorbital 2, only preserved in 38107, the sensory canal is not visible.

In infraorbital 3 the sensory canal runs parallel to the concave anterior margin of the bone. In P.154 it gives off two postero-ventrally directed tubules, the anterior

one rather short, and two posteriorly directed tubules. In 38107 there seem to be only three tubules, only one of them posteriorly directed; in the other specimens the state of preservation does not allow any observations regarding the tubules.

In infraorbitals 4 and 5 the sensory canal gives off a single, posteriorly directed tubule in each bone.

In the dermosphenotic, well preserved in 38107, the infraorbital sensory canal curves posteriorly; from its convex dorsal side the canal gives off a rather wide, dorsally directed tubule, ending in a pore; this pore is also visible on the defective dermosphenotic in P.1052*d*.

From the dermosphenotic the canal enters the dermopterotic, piercing it along its lateral margin. To what extent the canal in the dermopterotic belongs to the sensory canal system of the head and to the cephalic division of the main lateral line, respectively, must be left unanswered. Judging from P.3589*a* the posterior part of the canal gives off two dorsally directed short tubules, and the preopercular sensory canal seems to issue at the postero-lateral corner of the bone.

Cephalic division of main lateral line

A well-marked middle pit-line is visible in P.1052d on the left parietal posterior to the anterior pit-line; it extends laterally over the broad posterior part of the dermopterotic.

The cephalic division of the main lateral line passes over from the dermopterotic into the extrascapular, where it gives off mesially the supratemporal commissure, and continues posteriorly into the suprascapular. Because of the preservation of the extrascapular the canal and its tubules can be only partly observed ; in P.1052*d* two rather long tubules are given off from the lateral side of the canal, and at least four short tubules issue from the posterior side of the supratemporal commissure. In 38107 also, four short tubules are given off from the posterior side of the supratemporal commissure decreasing in length mesially, but in this specimen only one large tubule can be observed with accuracy lateral to the main canal.

The *preopercular sensory canal* runs on the whole parallel to the curved anterior margin of the preoperculum, about midway between its anterior and posterior margins in the dorsal limb but decidedly nearer to its anterior margin in its anteroventral limb. From its posterior side the canal gives off a series of tubules the number and arrangement of which are difficult to determine with precision in the largest specimens because of the thickness of the bone, especially in the dorsal limb of the bone; in the small specimens the preoperculum is too defective to allow any detailed analysis of number and position of the tubules, but their arrangement seems to be generally the same as in the larger specimens. In the antero-ventral limb of the preoperculum there are in 25276, 38107, and 38109 thirteen postero-ventrally directed, curved tubules increasing in length from the anterior small one to the twelfth; the thirteenth tubule is shorter and does not reach the postero-lateral margin of the bone. In P.1051 there is the same characteristic arrangement of the tubules, but their number cannot be counted with accuracy.

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group of tubules the tubules are shorter and seem to vary a little in number and position. 25276 clearly shows six rather short tubules, in 38109 only five tubules can be observed, but the dorsalmost part of the bone is defective ; in 38107 and P.154 at least 4 short tubules are present, but also here their exact number is difficult to determine. In P.1051, in which the preoperculum is remarkably thick and, moreover, broken in its dorsal part, only three short tubules can be seen. The real number of small tubules in the dorsal part of the preoperculum may be estimated as five or six and the total number of tubules belonging to the preopercular sensory canal may consequently be given as 18–19.

On the lateral surface of the preoperculum at about its middle and anterior to the preopercular sensory canal two short grooves are clearly visible in most specimens, the dorsal one more or less horizontal, the ventral one on the whole vertical. It seems most likely that the horizontal groove represents the posterior portion of the anterior division of the supramaxillary line and the vertical one the post-maxillary line according to the nomenclature proposed by Stensiö (1947). In P.154, however, no supramaxillary line can be observed on the preoperculum, but on infraorbital 3 an oblique groove is present, which may be interpreted as the anterior portion of the anterior division of the supramaxillary line. This difference in the development of the supramaxillary line may merely be an individual variation rather than a feature of taxonomic importance.

The *mandibular sensory canal* and its tubules are not visible, only the openings of some separate tubules may be observed, but their total number cannot be determined.

In the largest specimen investigated, 25276, as well as in the small specimens 39859 and P.154, there is a small vertical groove on the lateral surface of the angular near its ventral margin; this groove obviously represents the oral line according to Stensiö (1947).

Exoskeletal shoulder girdle and squamation

The *suprascapula* (Ssc, Pl. 1) is partly visible in 38107 and P.1052*d*, but in neither case can its outline be determined; it is, however, a rather large bone. In 38107 a smaller, reniform bone postero-ventral to the suprascapula may be the *supracleithrum*, but no sensory canal can be observed in it.

The *cleithrum* is only to a small extent exposed in the material studied by me and no description can be given.

The *scales* are, according to Woodward (1895), arranged in approximately 40 transverse rows; in none of the specimens seen by me is the squamation uninterrupted but in 38107 there may be about 45 transverse rows reckoned from the posterior margin of the operculum to the middle of the caudal fin. On the body there are about four longitudinal rows of scales which are deeper than broad, the lateral line scales being the deepest. All scales have an even posterior margin.

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Lateral line

The parts of the lateral line piercing the suprascapula and the supracleithrum are not visible in any of the specimens exhibiting these bones, and in the supracleithrum no tubules can be observed. In the suprascapula two rather wide tubules are clearly visible, the anterior one mesially, the posterior one postero-mesially directed.

The lateral line runs almost straight along the sides of body and tail, ending at the base of the middle caudal rays. Each lateral line scale has a pore at about the middle of its lateral surface.

Paired and unpaired fins

The fins are as a rule more or less defective in all specimens investigated by me and consequently little can be added in this respect to the facts given by Woodward (1895:451).

The *pectoral fin* seems to be of moderate size and with a moderate number of lepidotrichia, about 18 according to my counts, i.e. the same number as given by Woodward for the pectoral. The first lepidotrichium is rather stout and is provided with some fulcra.

The *ventral fin* has a rather high number of lepidotrichia, about 14 or 15 (14 according to Woodward), the innermost ones rather delicate and branched almost to their bases. The first two lepidotrichia are comparatively short and undivided, the third one (the first branched lepidotrichium) carries some fulcra.

The *dorsal fin* has, according to Woodward, about 12 lepidotrichia ; in my material no dorsal fin is complete. In P.154 the anterior part of the fin is rather well preserved and shows anteriorly three undivided lepidotrichia followed by a long divided lepidotrichium with few but rather long fulcra.

Regarding the *anal fin* Woodward gives no number of lepidotrichia, and in my material all anal fins are damaged and incomplete. On none of them have I observed any traces of fulcra, but as Woodward mentions the presence of fulcra on all fins, he must have seen some on the anal fin also.

The *caudal fin* is hemi-heterocercal and provided with densely set fulcra on its dorsal as well as on its ventral margin.

REMARKS. Woodward (1895: 450) considers *Ph. onychius* Agassiz to be identical with *Ph. bechei*. I have had no opportunity to see the holotype of *Ph. onychius*, belonging to the Oxford Museum, but 38109, originally labelled as *Ph. onychius* is, as far as I can see, in all respects a quite typical *Ph. bechei*, which supports Woodward's opinion.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset. Geol. 11, 8

Pholidophorus latiusculus Agassiz

(Pl. 4; Pl. 5; Pl. 15, figs. 1, 2, 6, 7; Text-figs. 3, 4)

1832 Pholidophorus latiusculus Agassiz : 145.

1833 Pholidophorus latiusculus Agassiz; Agassiz, 2:9.

1844 Pholidophorus latiusculus Agassiz; Agassiz, 2, 1: 271, 287.

1866 Pholidophorus latiusculus Agassiz; Kner: 328, pl. 3, figs. 2, 3.

1867 Pholidophorus latiusculus Agassiz; Kner: 903, pl. 2, fig. 1.

1895 Pholidophorus latiusculus Agassiz; (partim?) Woodward: 454, ? pl. 14, fig. 3.

PRELIMINARY DIAGNOSIS. *Pholidophorus* of small size, up to about 85 mm. in total length. Nasal not very large, anteriorly pointed. Posterior margin of preoperculum with a shallow notch. Preopercular sensory canal with about 14–15 tubules.

NEOTYPE. As already mentioned in the introduction, Agassiz did not name a holotype for this species. A species with this name is, however, described and figured by Kner (1866); the best preserved of his specimens, figured on Pl. 15, fig. 2, is still present in the collections of the Univ. Institut für Geologie und Paläon-tologie, Innsbruck, Austria, and may conveniently be chosen as neotype of *Pholidophorus latiusculus*. The correctness of the identification is beyond doubt as can be seen by a comparison between the figure given by Kner (represented on Pl. 15, fig. 1) and a photograph in natural size of the same specimen (Pl. 15, fig. 2).

MATERIAL. The description given below is based on the following specimens: Three specimens, F.123 (neotype), Lit. F and No. 1028, all belonging to the Univ. Institut für Geologie und Paläontologie, Innsbruck, and two specimens, 33987 (in counterpart) and P.1063, both belonging to the Department of Palaeontology, British Museum (Natural History); further, a rather disarticulated specimen, P.11780, showing a number of scales and some isolated cranial bones may also belong to this species or perhaps to *Ph*. cf. *pusillus*.

DESCRIPTION. All the specimens, except P.II780, show the same characteristic shape, with the head and forepart of the body bent dorsally. The three Innsbruck specimens are of about the same size with a length without caudal (standard length) of ca.75 mm.; in the neotype the caudal fin is defective, in the two other specimens the caudal fin has a length of ca. 10 mm.; the total length may consequently attain ca.85 mm. Specimens 33987 and P.IO63 are smaller; the first with a total length of ca.75 mm. and a standard length of ca.65 mm., P.IO63 with a standard length of ca.57 mm. The greatest depth of the body cannot be given as all specimens are more or less flattened through pressure. The length of the head seems to be roughly one quarter of the standard length.

Exoskeletal skull roof

The snout region is defective in all specimens available and the premaxillary and rostral bones are missing.

The nasal (Na, Pl. 4; Pl. 5, fig. 1; Text-figs. 3, 4) is preserved only in the neotype and in P.1063; it is comparatively large but its anterior part is pointed, not broadly



FIG. 3. Pholidophorus latiusculus Agassiz. Attempted restoration of head in lateral view. \times 7 approx.

Ang, angular; De. Spl, dentary; Dpt, dermopterotic; Dsph, dermosphenotic; Ext, extrascapular; Fr, frontal; Ifo_1-Ifo_5 , infraorbitals 1 to 5; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pa, parietal; Pop, preoperculum; Sbo, suborbital; Smx_1 , Smx_2 , anterior and posterior supramaxillaries; So_1 , So_2 , anterior and posterior supraorbitals; Sop, suboperculum; ap, anterior pit-line; hc_1 , anterior division of supramaxillary pit-line; ifc, infraorbital sensory canal; mp, middle pit-line; orp, postmaxillary pit-line; orp_1 , oral pit-line; poc, preopercular sensory canal; soc, supraorbital sensory canal.

rounded as in *Ph. bechei* and the bone is not pierced by the posterior nasal opening. Its dorso-lateral surface is ornamented with irregular streaks and tuberculations.

The *frontal* (Fr, Pl. 4; Pl. 5, figs. 1, 2; Text-figs. 3, 4) has on the whole the same shape as in *Ph. bechei*, but its anterior part, mesial to the nasal, seems to be comparatively more slender. As in that species the suture between the frontals of both sides is straight anteriorly but in the middle of its course somewhat sinuous; in P.1063 (Pl. 5, fig. 1) it curves at first a little to the left, then to the right and then again to the left. The entire dorsal surface of the frontal carries small ganoin rugosities which form low radiating ridges in its antero-lateral part.

The two *supraorbitals* (So_1 , So_2 , Pl. 4; Pl. 5, fig. 1; Text-figs. 3, 4) are of about the same size. The anterior one, supraorbital 1, is situated posterior to the nasal; in P.1063 its anterior part is hidden below the posterior part of the nasal, but judging from the neotype its anterior part is rounded off, not drawn out into an antero-lateral

projection as in *Ph. bechei*. The mesial margin of supraorbital 2 slightly overlaps the lateral margin of the frontal; posteriorly its lateral margin is concave, fitting the antero-dorsal margin of the dermosphenotic. Both supraorbitals are ornamented with low ganoin ridges and rugosities.

The *dermosphenotic* (*Dsph*, Pl. 5, fig. 1; Text-figs. 3, 4) is, judging from P.1063, a rather small bone, pointed anteriorly and rounded posteriorly with its dorsal margin a little convex and its antero-ventral margin a little concave.

The *parietal* (*Pa*, Pl. 5, fig. 1; Text-figs. 3, 4) and the *dermopterotic* (*Dpt*, Pl. 4; Pl. 5, figs. 1, 2; Text-figs. 3, 4) cannot be described in detail because of the bad state of preservation which does not allow a determination of their boundaries.

Only the lateral part of the *extrascapular* is preserved in P.1063 (*Ext*, Pl. 5, fig. 1). Apparently it is pushed over the posterior part of the dermopterotic, and consequently nothing can be made out with regard to its general shape.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pl. 4; Pl. 5, fig. I; Text-fig. 3) is defective in all specimens but to judge from 33987 it is pointed anteriorly, rather as in *Ph. bechei*, and then deepens with its deepest part at its posterior rounded end. Its dorsal margin is slightly concave and is overlapped by infraorbital I (lachrymal) and the two supramaxillaries. The lateral surface of the maxillary is provided with a dense longitudinal striation. Along the whole slightly convex ventral margin there is a feeble dentition like that in *Leptolepis*.

The two supramaxillaries $(Smx_1, Smx_2, Pl. 4; Pl. 5, fig. 1; Text-fig. 3)$ overlap the posterior part of the dorsal margin of the maxillary. The anterior one, supramaxillary 1, best preserved in the neotype (Pl. 4), is comparatively small, semicircular to almost triangular in shape; its lateral surface is ornamented with well-marked concentric ridges or streaks. Among the few cranial bones preserved in P.11780 there is a small semi-circular bone with a marked striation, which agrees rather well with supramaxillary 1 in the neotype. Supramaxillary 2 is fairly large and elongate with its dorsal and ventral margins slightly convex; posteriorly it is rounded off; its antero-ventral margin is concave, fitting the postero-dorsal margin of supramaxillary 1. The antero-dorsal tip of supramaxillary 2 is slightly thickened but not markedly produced. Its lateral surface is ornamented with numerous wellmarked striations running parallel to its dorsal and ventral margins; they are partly confluent in the middle of the bone.

Unfortunately, of the bones of the infraorbital series, the antorbital is missing in all specimens investigated.

Infraorbital 1 (lachrymal) (If o_1 , Text-fig. 3) is present only in 33987 and there only as a fragment of its anterior part; nothing therefore can be made out with regard to its general shape.

Infraorbital 2 (If o_2 , Pl. 5, fig. I; Text-fig. 3) is preserved in P.1063; it is, as usual, a small elongate bone which is situated below the orbit; its posterior margin is postero-ventrally directed.



FIG. 4. *Pholidophorus latiusculus* Agassiz. Attempted restoration of head in dorsal view (possibly somewhat flattened). ×7 approx. Lettering as in Fig. 3.

Infraorbital 3 (Ifo₃, Pl. 4; Pl. 5, figs. r, 3; Text-fig. 3) stretches from the orbit to the anterior margin of the preoperculum, which it overlaps as in *Ph. bechei*; its general shape is also almost as in that species.

Infraorbital 4 (If o_4 , Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) has its anterior, dorsal and ventral margins almost straight whereas its posterior margin is slightly convex; it is about half as broad as infraorbital 3.

Infraorbital 5 (Ifo₅, Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) can only be seen in part in the neotype, in P.1063 and, in impression, in Innsbruck Lit. F; it seems to have about the same general shape as infraorbital 4.

The suborbital (Sbo, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) seems to be a little broader than in *Ph. bechei*. Judging from the neotype its anterior margin lies almost vertical, whereas its posterior margin is slightly curved in the antero-ventral direction.

The preoperculum (Pop, Pl. 4; Pl. 5, figs. 1, 3; Text-fig. 3) is best preserved in the neotype, where it is partly hidden below infraorbital 3 and the suborbital, in P.1063 and, in impression, in Innsbruck Lit. F, where its postero-ventral part is lost. In 33987 it is rather defective. Its general shape resembles that of the pre-operculum in *Ph. bechei*, but its dorsal limb is broader and its postero-ventral part

does not protrude posteriorly as in that species ; the notch in its posterior margin is consequently much shallower. It is not possible to determine the course of the anterior margin of the preoperculum because of the overlying bones, but judging from the impression in Innsbruck Lit. F, the anterior margin has a slight convexity ventral to the middle of its length (Pl. 5, fig. 3). In P.II780 there is a fragmentary bone which I interpret as the left preoperculum ; its anterior margin is rather well preserved and shows the same convexity as in the specimen just mentioned.

The operculum (Op, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) has, on the whole, the same general shape as in *Ph. bechei*, but its dorsal part seems to be broader and its ventral tip is more obtuse; its anterior margin is a little thickened except ventrally where the margin is slightly notched for the antero-dorsal process of the suboperculum.

The suboperculum (Sop, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) seems to be proportionately as large as in *Ph. bechei* but its posterior margin is defective in all specimens except P.11780, possibly belonging to this species; in this specimen its posterior, wellpreserved part shows a shallow concavity high on the posterior margin.

Of the *interoperculum* (*Iop*, Pl. 4; Pl. 5, fig. 1; Text-fig. 3) only the posterior part is visible in the neotype, in P.11780 and, in impression, in Innsbruck Lit. F.

Branchiostegal rays and gular plate

The branchiostegal rays and the gular plate cannot be seen in any of the available specimens.

Lower jaw

The lower jaw is only partly exposed in the neotype and in 33987 and P.1063; in Innsbruck Lit. F. the left lower jaw is exposed but very defective (Pl. 15, fig. 6) and in P.11780, possibly belonging to this species, an isolated right lower jaw is present but partly crushed (Pl. 15, fig. 7). These specimens suggest that the lower jaw in *Ph. latiusculus* has about the same shape as in *Ph. bechei* (Pl. 13, fig. 5).

In all the specimens of *Ph. latiusculus* the ventral, splenial part of the *dentary* is separated from the dorsal, dental part by a well-marked ridge and its lateral surface is ornamented with thick ganoin rugosities and irregular striations. The dental part is anteriorly only gently ascending but further back it bends dorsally to form a small process, and then runs postero-dorsally; its lateral surface is without ornamentation. No teeth can be observed.

The limit between the dentary and the *angulo-supra-angular* (Ang, Pl. 15, fig. 7) is not clearly visible. The postero-ventral part of the lateral surface of the last named bone carries a well developed ornamentation.

Sensory canal system of head

The sensory canal system of the head seems to follow the same general pattern as in *Ph. bechei*, as far as the preservation of the material allows a comparison.

The supraorbital sensory canal (soc, Pl. 5, fig. 1; Text-figs. 3, 4) pierces the nasal, the frontal and the parietal.

In the nasal the canal runs almost straight from the antero-lateral to the posteromesial part of the bone in P.1063; no tubules or pores can be observed. In the neotype this part of the canal is not clearly visible.

In the frontal the supraorbital sensory canal is rather well-marked as a slight ridge on the dorsal surface of the bone. Its course is on the whole the same as in Ph. bechei : an anterior part running almost straight posteriorly is followed by a curved part corresponding to the broadening of the frontal; the posterior part runs at first in postero-mesial direction, then straight back to the middle of the posterior margin of the bone. P.1063 has the following arrangement of tubules and pores (Text-figs. 3, 4): from its anterior straight part the left canal gives off laterally two short tubules ; from its curved part three short tubules are given off from the mesial side ; the straight postero-mesially directed part has on its lateral side three very short tubules or pores; the posteriormost part of the sensory canal is damaged and the presence of pores or tubules in that part cannot be made out. On the right side corresponding tubules are given off from the anterior and the curved parts of the canal, but further back only a single pore or tubule on the mesial side of the canal can be observed. In Innsbruck Lit. F. (Pl. 5, fig. 2) there seem to be three laterally directed tubules issuing from the anterior straight part of the canal but only two pores from the curved part can be observed : along the lateral side of the posterior. postero-mesially directed part of the canal there are four pores.

The parietal part of the supraorbital sensory canal is well exposed in P.1063 (Pl. 5, fig. 1). It is comparatively much longer than in *Ph. bechei* and on the right parietal there is a small shallow concavity on the dorsal surface of the canal which may be a pore, but its interpretation as a true pore is questionable. The sensory canal continues posteriorly as a well-marked groove, the anterior pit-line (ap, Pl. 5, fig. 1; Text-figs. 3, 4).

The *infraorbital sensory canal* (*ifc*, Text-fig. 3) is quite unknown in its anterior parts because of the absence of the rostral and antorbital bones.

Only in 33987 is infraorbital I (lachrymal) present, and there only in its anteroventral part; it shows the anterior curved part of the canal in this bone with two antero-ventrally directed, pore-like tubules. For the rest the sensory canal and its tubules in infraorbital I are unknown.

In infraorbital 2 the sensory canal is not visible.

In infraorbital 3 the sensory canal pierces the bone parallel to its concave anterior margin. From its morphologically posterior side it gives off some tubules, the number of which is not easy to determine because of the thickness of the bone. In the neotype (Pl. 4) there seem, however, to be three rather long posteriorly directed tubules situated close together; antero-ventral to these tubules a short postero-ventrally directed tubule is present. In P.1063 (Pl. 5, fig. 1) only two long, posteriorly directed tubules can be seen with certainty; a short postero-ventrally directed tubule in the anterior part of the bone seems to be present but cannot be observed in detail.

In infraorbital 4 the sensory canal gives off posteriorly a single tubule in the neotype. In infraorbital 5, which is only partly visible, no tubule can be observed with accuracy.

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Judging from 33987, in which the posterior part of the dermosphenotic is preserved, the posteriorly curving sensory canal pierces this bone in its posterior part; from the anterior side of the curve a rather wide tubule is given off in antero-dorsal direction. In P.1063 the canal itself cannot be followed exactly, but the tubule is partly visible and seems to end in a pore at the dorsal margin of the bone.

The sensory canal passes over into the dermopterotic and runs along its lateral margin. Judging from specimen Innsbruck Lit. F it seems to give off dorsally two short tubules. As in *Ph. bechei* the preopercular sensory canal seems to be given off near the postero-lateral corner of the bone.

Cephalic division of main lateral line

The middle pit-line (mp, Pl. 5, figs. 1, 2; Text-figs. 3, 4) is well developed, stretching from the postero-mesial part of the parietal to near the lateral margin of the dermopterotic.

The cephalic division of the main lateral line passes over from the dermopterotic to the extrascapular, but as this bone is very badly preserved or missing nothing can be made out regarding this part of the canal and its tubules.

The preopercular sensory canal runs, as in Ph. bechei, on the whole parallel to the anterior margin of the preoperculum. The tubules given off from its morphologically posterior side show the same general pattern as in Ph. bechei. In the neotype, the best preserved specimen in this respect, there seem to be three short, almost straight tubules dorsal to the angle on the posterior margin of the bone, the dorsalmost difficult to observe with accuracy as it is hidden below the suborbital, and ventral to the angle two shorter, slightly curved tubules; these five dorsal tubules obviously correspond to the four to six shorter dorsal tubules in Ph. bechei. Ventral to these shorter tubules there is, as in *Ph. bechei*, a rather long tubule which, however, does not reach the posterior margin of the bone. Anteriorly it is followed by nine curved tubules which decrease in length antero-ventrally; there are thus ten openings belonging to this group of tubules, but it seems as if the fourth tubule reckoned from the antero-ventral tip of the preoperculum is only a branch of the following tubule. The ten antero-ventral tubules in question obviously correspond to the thirteen antero-ventral tubules in Ph. bechei. In P.1063 the shorter dorsal tubules are likewise five in number but the ventral part of the preoperculum is too damaged to allow a count of the tubules. The preopercular impression in Innsbruck Lit, F shows five dorsally situated shorter tubules and ventral to them about nine tubules. The total number of tubules belonging to the preopercular sensory canal in Ph. latiusculus is consequently 14-15 against 17-19 in Ph. bechei.

In P.1063 (Pl. 5, fig. 1) the lateral surface of the preoperculum shows one almost horizontal (hc_1) and one vertical (orp) groove, obviously the posterior portion of the anterior division of the supramaxillary line and the postmaxillary line respectively as described above in *Ph. bechei*. An oblique, posteriorly directed groove on the lateral surface of infraorbital 3 may represent the anterior portion of the anterior division of the supramaxillary line. In the neotype (Pl. 4) the postmaxillary line is hidden below infraorbital 3, but the other two lines are clearly visible, that on infraorbital 3, however, is not continuous but divided into two parts. In Innsbruck Lit. F. (Pl. 5, fig. 3) all the three lines mentioned can be traced on the impression. As compared with the corresponding lines in *Ph. bechei* the two lines on the preoperculum are proportionately much longer and the line on infraorbital 3 seems to occur normally in all specimens.

The mandibular sensory canal can partly be seen in the neotype and in P.1063; the openings of separate tubules, marked by ganoin thickenings, are visible here and there ventral to the ridge separating the dental and splenial parts of the dentary; their total number cannot be made out.

In 33987, the only one in which the lateral surface of the angular is clearly exposed, a small vertical groove representing the oral line is visible on the angular near its ventral margin.

Exoskeletal shoulder-girdle and squamation

A suprascapula cannot be identified in any of the specimens investigated. In the neotype an almost triangular bone with strongly marked ganoin ridges on its lateral surface may be a *supracleithrum* (Scl, Pl. 4). In the smaller specimen, 33987, the same bone is visible but the ganoin ridges are not as marked as in the neotype; in P.1063 (Pl. 5, fig. 1) a fragment of the same bone is present. In the last named specimen much of the *cleithrum* (Cl, Pl. 5, fig. 1) is exposed, and shows a large, deep notch above the insertion of the pectoral fin.

The squamation (Pl. 4) is only partly preserved, but in the neotype about 38 transverse scale rows can be observed, reckoned from the posterior margin of the operculum to the middle of the caudal fin base. The lateral line scales are the deepest, but also the rows immediately above and below the lateral line scales seem to be deeper than broad. All the scales are comparatively thick and have an even posterior margin.

Lateral line

Nothing can be made out regarding that part of the lateral line piercing the suprascapula and the supracleithrum. The lateral line scales are arranged in an almost straight row along the side of the body (l.l, Pl. 4; cf. also Pl. 15, fig. 2).

Paired and unpaired fins

Very little can be said regarding the fins in this species.

The *pectoral fin* is partly preserved in all specimens investigated but only in P.1063 can the number of lepidotrichia be counted with accuracy (Pl. 5, fig. 1); there seem to be about 19 lepidotrichia, the first one carrying some small fulcra.

Only a few lepidotrichia belonging to the *ventral fin* are preserved in specimen 33987, in others the ventral fin is missing.

The dorsal and anal fins are lacking in all specimens seen by me, but according to Kner (1867, pl. 2, fig. 1) the dorsal fin is situated approximately above the ventral fins as in *Ph. bechei*.

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The *caudal fin* is hemi-heterocercal and carries well-developed fulcra on its dorsal and ventral margins.

REMARKS. Apart from small differences, mainly in the ornamentation of the exoskeletal cranial bones, all the specimens mentioned above except P.11780 are so similar that they may be considered to belong to one and the same species. Whether the specimens from Italian localities attributed to *Ph. latiusculus* by authors such as de Alessandri, Bassani, Costa, Mariani etc., are identical with the specimens described above is a question which at present must be left open, as I have had no opportunity to see them.

HORIZON AND LOCALITY. Upper Trias; Seefeld, Tyrol, Austria.

Pholidophorus (?) caffii Airaghi

(Pl. 6, fig. 1; Text-fig. 5)

1908 Pholidophorus Caffii Airaghi : 3, text-fig. 2.

1914 Pholidophorus latiusculus Agassiz; (partim) Bassani: 379.

1920 Pholidophorus latiusculus Agassiz; (partim) Alessandri: 96.

1937 Pholidophorus latiusculus Agassiz; Boni: 132, pl. 4, fig. 4, pl. 5, fig. 3, text-figs. 9, 10.

DIAGNOSIS. *Pholidophorus* (?) of small size, up to 58 mm. in total length. Greatest depth of body about one quarter of the standard length or slightly more. Depth of caudal peduncle about one-tenth of the standard length. Maxillary and lower jaw rather short. Infraorbitals 3 and 4 deeper than broad. Preoperculum broad, its posterior margin without a marked notch. Preopercular sensory canal running nearer to posterior than to anterior margin of bone in dorsal limb, in ventral limb at about the middle, and with about eight tubules. Scales thick, not serrated posteriorly, arranged in about 35 transverse rows counted from posterior margin of operculum to middle of caudal fin base. A few longitudinal rows of body scales deeper than broad.

HOLOTYPE. Specimen originally described by Airaghi (1908) and belonging to the Museo Civico di Scienze Naturale di Bergamo, Italy. The only specimen.

DESCRIPTION. The total length of the holotype is 58 mm., the length from the tip of the snout to the hindmost lateral line scale (standard length) is 49 mm. The estimated depth of the body is slightly more than one quarter (26.5%) of the standard length and the depth of the caudal peduncle is about one-tenth of that length. The length of the head is estimated to be slightly less than one quarter of the standard length. The maxillary and lower jaw are, comparatively, a little shorter than in *Ph. bechei* and *Ph. latiusculus*.

The position of the paired and unpaired fins is clearly visible. The base of the ventral fin is situated a little nearer to the hindmost lateral line scale than to the tip of the snout, and the distance between the base of the ventral and the origin of the anal is about 75% of the distance between the bases of the pectoral and ventral fins. The dorsal fin begins above the ventral fin base. A good figure of the entire fish is given by Boni (1937, pl. 5, fig. 3).

The cranial bones are, unfortunately, partly defective ; most bones belonging to the exoskeletal skull roof are lacking and many of the other cranial bones are poorly preserved. Consequently the following description is rather incomplete.

Exoskeletal skull roof

The premaxillary, rostral, nasal, frontal, supraorbital, dermosphenotic and dermopterotic bones are missing or represented by insignificant fragments. Parts of the parietal and the extrascapular seem to be present (*Pa*?, *Ext*?, Pl. 6, fig. 1), but their shape cannot be made out.

Dermal bones of cheek and opercular apparatus

Only the posteriorly directed lateral part of the comparatively short *maxillary* is present $(Mx + Smx_1, Pl. 6, fig. I; Text-fig. 5)$. It is, however, very defective, almost the entire ventral part is missing and consequently nothing can be made out



FIG. 5. Pholidophorus (?) caffii Airaghi. Holotype. Attempted restoration of head in lateral view. \times 10.5.

Ang, angular; Ant, antorbital; De. Spl, dentary; Ifo_1-Ifo_5 , infraorbitals I to 5; Iop, interoperculum; $Mx + Smx_1$, maxillary and anterior supramaxillary; Op, operculum; Pop, preoperculum; Sbo, suborbital; Smx_2 , posterior supramaxillary; Sop, suboperculum; hc_1 , anterior division of supramaxillary pit-line; ifc, infraorbital sensory canal; mdc, mandibular sensory canal; orp, postmaxillary pit-line; orp_1 , oral pit-line; poc, preopercular sensory canal.

regarding the depth of the maxillary or of the dentition. The lateral surface of the preserved part is, however, ornamented with longitudinal streaks and, posteriorly, with some short oblique ridges. The posterior end of the maxillary is broken off, and thus its shape, if rounded or notched, cannot be stated. According to Boni (1937, text-fig. 9) the posterior part of the maxillary is wedged between infraorbital 3 and the antero-ventral limb of the preoperculum, but the part in question is, as far as I can see, the antero-dorsal part of the ventral limb of the preoperculum, and not part of the maxillary.

Boni's text-fig. 9 shows only a single supramaxillary, obviously corresponding to supramaxillary 2 in other species; anterior to it the figure shows, however, a roughly triangular or semicircular elevation on the dorsal margin of the maxillary, corresponding to supramaxillary I in other forms. At first I was inclined to consider this eminence as not belonging to that bone, but as soon as I had the opportunity of examining the holotype I could confirm that there was no division between this elevation and the rest of the maxillary. Whether this is a secondary, perhaps individual, fusion of the two bones or a primitive stage of development, characteristic of *Ph. caffii*, is a question which must be left open until more specimens of this species are available for study. Supramaxillary 2 (Smx_2 , Pl. 6, fig. I; Text-fig. 5) is rather well preserved; it is almost rectangular, its antero-dorsal corner forms a blunt short process, and its lateral surface is ornamented with rather dense, horizontal striations.

All the bones of the infraorbital series, an antorbital and five infraorbitals, are present.

The *antorbital* (*Ant*, Pl. 6, fig. 1; Text-fig. 5) is rather well preserved but its outline cannot be made out in detail; it is large in comparison with the antorbital in *Ph. bechei* and tapers postero-dorsally.

Infraorbital I (lachrymal) (If o_1 , Pl. 6, fig. I; Text-fig. 5) was exposed by preparation; it is rounded anteriorly, its ventral margin is convex, its dorsal margin concave and the exposed dorso-lateral surface is slightly concave.

Infraorbital 2 (Ifo₂, Pl. 6, fig. 1; Text-fig. 5) is well preserved but broken into two pieces; it has a generally elongate shape with the dorsal margin slightly concave, the ventral margin slightly convex.

Infraorbital 3 (Ifo₃, Pl. 6, fig. I; Text-fig. 5) is likewise well preserved except that its postero-dorsal corner is broken off; it is markedly deeper than broad and its dorsal margin constitutes an obtuse angle so as to fit the ventral margins of infraorbital 4 and the suborbital.

Infraorbital 4 (Ifo₄, Pl. 6, fig. 1 ; Text-fig. 5) is partly incomplete but seems to be a little deeper than broad.

Infraorbital 5 (If o_5 , Pl. 6, fig. 1; Text-fig. 5) is better preserved and seems to be almost square and only a little smaller than infraorbital 4.

Posterior to infraorbitals 4 and 5, the ventral part of the *suborbital* (*Sbo*, Pl. 6, fig. I; Text-fig. 5) is clearly visible but it is broken into two pieces on to the lateral crest of the hyomandibular; regarding its outline it can only be said that its posterior

margin seems to be straight and vertical, thus probably not overlapping the anterior margin of the operculum, and that its postero-ventral margin is a little convex.

The preoperculum (Pop, Pl. 6, fig. 1; Text-fig. 5) is, comparatively, very broad, especially in its antero-ventral limb, the antero-dorsal margin of which shows a rather pronounced convexity; the postero-ventral margin of the preoperculum is damaged but it seems to have been almost straight or only slightly concave and thus without the notch characteristic of the preoperculum in *Ph. latiusculus* and especially in *Ph. bechei*. The uppermost end of the preoperculum is defective.

The operculum (Op, Pl. 6, fig. 1; Text-fig. 5) seems to have the usual almost triangular shape, but as its anterior and dorsal margins are damaged its shape cannot be made out exactly. Its ventral tip is rounded, about as in *Ph. latiusculus*, and as in that species the anterior margin of the operculum is slightly notched ventrally to receive the antero-dorsal process of the suboperculum.

The suboperculum (Sop, Pl. 6, fig. I; Text-fig. 5) is only partly preserved; its antero-dorsal process is well developed.

The *interoperculum* (*Iop*, Pl. 6, fig. 1; Text-fig. 5) seems to be roughly triangular with the posterior margin slightly convex; its lateral surface carries a few striations parallel to its margins.

Branchiostegal rays and gular plate

The posteriorly situated, rather short but broad *branchiostegal rays* (R. Br, Pl. 6, fig. 1) are visible ventral to the preoperculum and the interoperculum.

The gular plate is not visible.

Lower jaw

The lower jaw is, like the maxillary, comparatively short. Anteriorly the dorsal margin of the dental part of the *dentary* (*De. Spl*, Pl. 6, fig. 1; Text-fig. 5) is only gently ascending, but as most of the dorsal margin of the lower jaw is covered by overlying bones, its outline cannot be followed. No teeth could be observed on the exposed dorsal margin of the dentary. The lateral surface of the dental part is smooth and that of the splenial part is only feebly ornamented but shows clearly the tubules of the mandibular sensory canal; the ridge separating the two parts of the dentary seems to be comparatively weak.

The ventral part of the *angular* (Ang, Pl. 6, fig. 1; Text-fig. 5) is well exposed; its lateral surface is practically smooth.

Sensory canal system of head

Regarding the sensory canal system of the head, almost nothing of the *supra*orbital sensory canal can be determined because the nasal and frontal bones are lacking. On the fragment thought to belong to the parietal a single short canal is visible. This might be interpreted as the posteriormost part of the supraorbital sensory canal, but as it is not followed by a pit-line this interpretation is rather uncertain. No canals, tubules or pores can be observed in the bone fragment considered as part of the extrascapular.

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The *infraorbital sensory canal (ifc*, Text-fig. 5) can be followed for almost its entire length; only the ethmoidal commissure and the part in the dermosphenotic and dermopterotic are missing. In the antorbital the canal describes an arch in its ventral part and gives off postero-dorsally an antorbital branch ending in a pore; at the point where the antorbital branch arises there seems to be a rather large pore. In infraorbital I (lachrymal) the sensory canal can be followed for most of its length but its state of preservation allows no statements regarding the number or disposition of its tubules. In infraorbital 2 the sensory canal is partly visible; an opening at the posterior end of the bone is not a real pore but an artifact due to damage. In infraorbital 3 the sensory canal gives off three postero-ventrally directed and short but strongly marked and widely separated tubules, the antero-ventral one being the shortest, the dorsal one the longest. The anterior part of infraorbital 4 is obviously pierced by the sensory canal, but no tubule can be seen with certainty. In infraorbital 5 the sensory canal can be traced but no tubule is visible.

Cephalic division of main lateral line

The *preopercular sensory canal* seems to pierce the dorsal limb of the preoperculum nearer to its posterior than to its anterior margin; in the ventral limb it runs at about the middle of its length, not nearer to its anterior margin as in *Ph. bechei* and *Ph. latiusculus*. The tubules given off from the morphologically posterior side of the canal are short but rather wide. Only eight tubules seem to be present, two in the dorsal limb of the preoperculum dorsal to and at the posterior angle of the bone respectively, one short tubule farther ventrally and five tubules in the ventral part of the ventral limb of the bone. Consequently, the general arrangement of the tubules is not unlike that in *Ph. bechei* and *Ph. latiusculus*, but the tubules in the ventral group are not long and narrow as in the two former species and the total number of tubules is only about 8 as against 17–19 in *Ph. bechei* and 14–15 in *Ph. latiusculus*.

On the lateral surface of the preoperculum there are two grooves, one horizontal and one vertical, $(hc_1, orp, \text{Pl. 6}, \text{fig. 1}; \text{Text-fig. 5})$, meeting at a right angle; the horizontal groove represents the posterior portion of the anterior division of the supramaxillary line and the vertical one the postmaxillary line according to the nomenclature proposed by Stensiö (1947).

The mandibular sensory canal (mdc, Pl. 6, fig. I; Text-fig. 5) is exposed to a small extent in the anterior, broken portion of the splenial part of the dentary; it is impossible to say how many tubules the canal gives off in that part of the bone, but posterior to the exposed part of the canal five short tubules are visible. Near the ventral margin of the angular there is a pore belonging to that part of the mandibular sensory canal which pierces the angular, and dorsal to this pore there is a short, vertical groove, representing the oral line (orp_1 , Pl. 6, fig. I; Text-fig. 5).

Exoskeletal shoulder-girdle and squamation

Dorsal to the operculum there is a large *suprascapula* (Ssc, Pl. 6, fig. 1) but it is crushed and partly defective and consequently its outline cannot be determined

exactly. Postero-ventral to it there is a *supracleithrum* (*Scl*, Pl. 6, fig. 1) of about the same size and shape as the suprascapula, but this bone also is crushed and defective. Almost the entire *cleithrum* is missing but its impression suggests a rather robust bone. Posterior to this impression there is a deep bony plate which may be interpreted as a *postcleithrum*.

The scales are arranged in about 35 transverse rows counted from the posterior margin of the supracleithrum to the middle of the caudal fin base (=lateral line scales). On the body the lateral line scales and those in the longitudinal rows immediately dorsal and ventral to them, three rows in all, are deeper than broad. All the scales are comparatively thick and, as far as can be judged, with a regular posterior margin.

Lateral line

Those parts of the lateral line piercing the suprascapula and the supracleithrum are not visible; in the suprascapula, however, a short but rather wide, mesially directed tubule can be seen; in the supracleithrum no tubules are visible.

The lateral line scales (l.l, Pl. 6, fig. 1) are arranged in a straight row from the second scale to the last one at the base of the middle caudal rays.

Paired and unpaired fins

All fins are present but at least in part more or less defective.

The pectoral fin is of moderate size. Boni (1937) gives the number of its lepidotrichia as 11, a remarkably low number. There are, indeed, 11 rather stout lepidotrichia clearly exposed, but ventral to the postcleithrum and easily overlooked there is a cluster of broken, more slender lepidotrichia; these may represent the posterior rays of the pectoral fin and their number may be at least 7–8, and consequently the total number of pectoral lepidotrichia may be estimated as about 18 or about the same number as in *Ph. bechei* and *Ph. latiusculus*. The first lepidotrichium carries some very small fulcra (*Fu*, Pl. 6, fig. 1).

The ventral fin is rather defective. For this fin Boni gives the number of lepidotrichia as 5, which is too low; as far as I can see there are at least two small, undivided lepidotrichia anteriorly, followed by 6 divided and branched lepidotrichia, the anterior one fulcrated. Posterior to these lepidotrichia the fin is damaged and the total number of ventral fin lepidotrichia thus remains unknown.

The *dorsal fin* is well preserved but the number of lepidotrichia is difficult to interpret. Anteriorly there are two undivided lepidotrichia, the anterior one rather short and almost scale-like; there follows a third, rather long, apparently undivided lepidotrichium with a comparatively long and slender rod (fulcrum?) in front of it; posterior to these three there are 8 divided and branched lepidotrichia, the anteriormost of which is richly fulcrated. Consequently, the total number of dorsal fin lepidotrichia is at least II as compared with 9 (IO?) as stated by Boni.

The *anal fin* is not as well preserved as the dorsal fin and the number of its lepidotrichia cannot be stated with accuracy. There are, however, two short, undivided lepidotrichia anteriorly followed by at least 7 divided and branched ones, the anteriormost of which with a few, long fulcra; thus there are at least 9 lepidotrichia as against the 5-6 as stated by Boni.

The *caudal fin* is hemi-heterocercal and its dorsal as well as its ventral margin is densely set with fulcra.

REMARKS. *Pholidophorus caffii*, described as a new species by Airaghi (1908), has been considered merely a synonym of *Ph. latiusculus* by Bassani (1914), de Alessandri (1920) and Boni (1937). It is, however, beyond doubt that the specimen on which Airaghi founded his species, redescribed above, does represent a species clearly distinguishable from *Ph. latiusculus* in the sense of Kner. Differences in the relative length of maxillary and lower jaw, the general shape of the preoperculum, the course of the preopercular sensory canal and the number of its tubules clearly separate Airaghi's *Pholidophorus caffii* from Kner's *Ph. latiusculus*. In my opinion differences in the preoperculum and the course of the preopercular sensory canal are of such a degree that the placing of *caffii* in the genus *Pholidophorus* s. str.may even be questionable. This problem will be discussed in more detail later on (p. 423).

HORIZON AND LOCALITY. Upper Trias; Viciarola, near S. Pellegrino (Val Brembana), Italy.

Pholidophorus cf. pusillus Agassiz

(Pl. 6, fig. 2; Text-fig. 6)

1895 Pholidophorus latiusculus Agassiz; Woodward: 455 (partim).

PRELIMINARY DIAGNOSIS. *Pholidophorus* of small size, up to 65 mm. in total length, similar to *Ph*. (?) *caffii* but differing from that species *i.a.* in the following features : Maxillary and lower jaw not markedly short. Infraorbitals 3 and 4 considerably broader than deep. Preoperculum similar to that of *caffii* but preopercular sensory canal with about 11 tubules, longer than those in *caffii*. Scales arranged in about 38-40 transverse rows counted from posterior margin of operculum to middle of caudal fin base.

MATERIAL. Specimen No. P.4418 in the Department of Palaeontology, British Museum (Natural History).

DESCRIPTION. The total length of the specimen is about 65 mm., the standard length is estimated as 56 mm. The greatest depth of the body cannot be determined. The depth of the caudal peduncle is about one-tenth of the standard length. The length of the head is estimated to be slightly less than one quarter of the standard length. The maxillary and lower jaw are relatively longer than in *Ph. bechei* and *Ph. latiusculus*, and even more so than in *Ph.* (?) caffii.

The fins are not preserved except for some lepidotrichia of the anal fin and the entire caudal fin ; the position of the dorsal fin in relation to the ventral fins is thus unknown.

The cranial bones are very defective; all bones belonging to the exoskeletal skull roof are lacking and many of the other cranial bones are fragmentary. Thus only the following rather incomplete description can be given.

Dermal bones of cheek and opercular apparatus

Only the posteriorly directed part of the comparatively long maxillary (Mx, Pl. 6, fig. 2; Text-fig. 6) is preserved; apart from its relatively greater length it seems to have the same general shape as in *Ph. bechei* and *Ph. latiusculus*, but its ventral margin is defective and consequently nothing can be said about its real depth or about the dentition. Neither can it be determined with any accuracy whether its posterior margin is rounded or slightly notched; judging from an impression on the preoperculum behind the broken end of the maxillary it looks, however, as if its posterior margin was slightly notched. The lateral surface of the maxillary is richly ornamented with ganoin spots and irregular longitudinal streaks and ridges except along its postero-dorsal margin, indicating that supramaxillary 2 may overlap the maxillary a little.

Of the supramaxillaries, supramaxillary I (Smx₁, Pl. 6, fig. 2; Text-fig. 6) is almost semicircular; it is well separated from the maxillary, but seems not to overlap the dorsal margin of that bone; its lateral surface carries a striation approximately parallel to the convex dorsal margin of the bone, similar to the striation on the dorsal



FIG. 6. Pholidophorus cf. pusillus Agassiz. Attempted restoration of head in lateral view. B.M. No. P.4418. $\times10$

Ang, angular; De. Spl, dentary; Ifo_1 , Ifo_3 , Ifo_4 , infraorbitals 1 and 3-4; Iop, interoperculum; Mx, maxillary; Op, operculum; Pop, preoperculum; Sbo, suborbital; Smx_1 , Smx_2 , anterior and posterior supramaxillaries; Sop, suboperculum; poc, preopercular sensory canal. GEOL. 11, 8 34 elevation of the maxillary in Ph. (?) caffii. Supramaxillary 2 (Smx_2 , Pl. 6, fig. 2; Text-fig. 6) has about the same, almost rectangular shape as in that species but it is comparatively longer antero-posteriorly; its antero-dorsal corner is broken off but may have been of about the same shape as in Ph. (?) caffii. The lateral surface of supramaxillary 2 shows a horizontal striation, but this striation is by no means as dense as in Ph. (?) caffii or in Ph. latiusculus.

The bones of the infraorbital series are only partly preserved.

An isolated bone fragment in the snout region looks like an *antorbital (Ant?*, Pl. 6, fig. 2), but this interpretation is rather uncertain.

Another bone fragment dorsal to the anteriormost preserved part of the maxillary may belong to *infraorbital* I (*lachrymal*) (*Ifo*₁, Pl. 6, fig. 2) but it provides no information about the outline of this bone.

Infraorbital 2 is missing.

Infraorbital 3 (Ifo₃, Pl. 6, fig. 2; Text-fig. 6) is remarkably broad, about twice as broad as deep, its postero-dorsal part overlaps the preoperculum and its dorsal margin is slightly concave; its shape is thus quite different from that of the corresponding bone in Ph. (?) caffii.

Infraorbital 4 (Ifo₄, Pl. 6, fig. 2 ; Text-fig. 6) is almost complete, nearly rectangular and considerably broader than deep.

Some bone fragments dorsal to infraorbital 4 indicate the presence of an *infra*orbital 5.

Between the visible part of the hyomandibular and the anterior margin of the operculum there is a rather large bony plate which is obviously a *suborbital* (Sbo, Pl. 6, fig. 2; Text-fig. 6); its margins are, however, only partly visible.

The *preoperculum* (*Pop*, Pl. 6, fig. 2; Text-fig. 6) is well preserved, only its uppermost end is defective. Its shape is very similar to that of the preoperculum in *Ph.* (?) *caffii*. A shallow concavity is present ventral to the ill-defined posterior angle between the upper and lower limbs of the bone, but there is no real notch as in *Ph. bechei* and *Ph. latiusculus*.

The operculum (Op, Pl. 6, fig. 2; Text-fig. 6) seems to be remarkably broad, much broader than in the other species treated here, but this may be partly due to pressure as the bone is somewhat dislocated.

The suboperculum (Sop, Pl. 6, fig. 2; Text-fig. 6), likewise dislocated, is only partly preserved; its postero-dorsal half is missing.

Of the *interoperculum* (*Iop*, Pl. 6, fig. 2; Text-fig. 6) only the posterior part is exposed; it seems to have the same general shape as in Ph. (?) caffii, but lacks the concentric striations.

Branchiostegal rays and gular plate

As in Ph. (?) caffii only some of the posterior branchiostegal rays (R. Br, Pl. 6, fig. 2) are exposed; they are, however, relatively much longer than in that species.

The gular plate is not visible.

Lower jaw

The lower jaw is exposed to a certain extent, but its anterior part is lacking and its dorsal margin is covered by the maxillary bones and cannot be described. It is, however, obvious that the lower jaw is relatively much longer and stouter than in *Ph.* (?) *caffii.* The lateral surface of the dental part of the *dentary* (*De. Spl.*, Pl. 6, fig. 2; Text-fig. 6) is quite smooth, whereas the splenial part, which seems to be deeper than in the three species described above, has a rich ganoin ornamentation obscuring the tubules of the mandibular sensory line; the ganoin-covered ridge separating these two parts of the dentary is very pronounced. No dentition could be observed.

The angular part of the *angulo-supra-angular* is partly visible but its posterior margin is indistinct because of damage ; its lateral surface is ornamented ventrally with ganoin patches.

Sensory canal system of head

Very little of the sensory canal system of the head can be made out. All the bones containing the *supraorbital sensory canal* are absent and only some parts of the *infraorbital sensory canal* are preserved (Text-fig. 6). In infraorbital 3 the sensory canal can be traced but the tubules are difficult to observe; there are, however, traces of at least two rather long, posteriorly directed tubules, and a third, very short tubule is given off from the anterior part of the canal. In infraorbital 4 the canal itself cannot be seen with accuracy, but a single large, posteriorly directed tubule is clearly visible.

Cephalic division of main lateral line

Of this part of the sensory canal system only the preopercular sensory canal is visible (Text-fig. 6). The canal itself pierces the preoperculum at about the middle of its length and, on the whole, lies parallel to its anterior and posterior margins, thus not nearer to its posterior margin in the dorsal limb as it is in Ph. (?) caffii and not distinctly nearer to its anterior margin as in Ph. bechei and Ph. latiusculus. The number of tubules given off from the posterior side of the canal is difficult to determine, but two tubules are clearly visible in the dorsal limb of the bone, dorsal to and at its posterior angle respectively; ventral to this angle there is a rather short tubule followed more ventrally by about eight wide tubules in the antero-ventral third of the bone. Between the second and the third tubules reckoned from above there is a structure resembling a postero-dorsally directed tubule or rather, a sensory line; its position posterior to the preopercular sensory line may be an argument against the interpretation of it being a supramaxillary line, but as it cannot be followed anteriorly because of the damaged condition of the lateral surface of the middle part of the preoperculum the question of its real nature must be left open. The same is true of the postmaxillary line, the ventralmost part of which may perhaps be traced ventral to the damaged middle part of the bone (orp?, Pl. 6, fig. 2). The total number of tubules belonging to the preopercular sensory canal may consequently be eleven, perhaps twelve, that is, only a little higher than in Ph. (?) caffii; their arrangement is virtually identical in the two species but those of the ventral group are considerably longer, almost reaching the ventral margin of the preoperculum; they are, however, not as long and as numerous as in Ph. bechei or Ph. latiusculus.

The *mandibular sensory canal* is not visible and only two tubular openings can be traced posteriorly on the splenial part of the dentary.

A short vertical groove on the lateral surface of the angular is probably an oral pit-line (orp, Pl. 6, fig. 2).

Exoskeletal shoulder-girdle and squamation

No bones belonging to the exoskeletal shoulder-girdle are visible.

The scales are comparatively thick with even posterior margins. There seem to be about 38-40 transverse rows of scales, counted from the posterior margin of the operculum to the middle of the caudal fin base, but as the squamation is in part rather badly damaged, this count is somewhat uncertain. On the anterior part of the body there are some longitudinal rows of scales which are deeper than broad. The dorsal margin of each body scale is drawn out into a peg (Sc, Pl. 6, fig. 2).

Paired and unpaired fins

The pectoral, ventral and dorsal fins are missing and only a few lepidotrichia of the anal fin are partly visible.

The caudal fin is hemi-heterocercal; its dorsal margin carries a dense series of rather large fulcra; along the ventral margin of the caudal fin the fulcra are smaller.

REMARKS. The specimen just described, identified by Woodward (1895) as Pholidophorus latiusculus, cannot belong to that species, or to Ph. (?) caffii, as is evident from the descriptions given above. On the contrary it seems to me rather probable that it may be identical with the second *Pholidophorus* species originally mentioned by Agassiz (1832) from Seefeld, Ph. pusillus, the material of which belonged to Dr. Alex. Braun and the Karlsruhe Museum. Dr. Erwin Jörg, Landessammlungen für Naturkunde, Karlsruhe, has kindly informed me that no material of Ph. pusillus or of Ph. latiusculus now exists in this collection; it was probably destroyed in 1942. The original material of Ph. pusillus must also be considered lost. The identification of Ph. pusillus proposed by Kner (1866) refers to some small fish specimens from Seefeld; in the Univ.-Institut für Paläontologie und Geologie, Innsbruck, some material exists which can be identified as the two upper specimens figured by him on pl. 6, fig. 2 (in reality the specimen b on this figure is composed of two specimens!). Their preservation is, however, rather poor, and they show no details (except some branchiostegal rays) which can be directly compared with those preserved in P.4418. But there are some facts favouring the identification of this specimen with Ph. pusillus. The size and slender shape of the body is about the same and according to Kner the number of transverse scale-rows amounts to 38-40, just as I have found in
the specimen in question. Because of this it seems to me rather improbable that two different *Pholidophorus* species of about the same size and shape should exist in the Seefeld deposits. Specimen P.4418 is most probably an unusually wellpreserved, large specimen of *Ph. pusillus*. A final decision as to its relationship with that species must, however, be postponed until more extensive and better preserved material from Seefeld can be thoroughly investigated. Therefore I have only identified the specimen in question as *Ph.* cf. *pusillus* Agassiz.

HORIZON AND LOCALITY. Upper Trias; Seefeld, Tyrol, Austria.

Genus PHOLIDOLEPIS nov.

PRELIMINARY DIAGNOSIS. Pholidophoridae of rather small size, as far as known similar to *Pholidophorus* but differing in the following features. Exoskeletal cranial bones with very feeble ganoin covering. Supramaxillary 2 with rather well-marked process at antero-dorsal corner. Preoperculum with preopercular sensory canal running near to anterior margin. Fulcra as far as known absent on all fins except along dorsal margin of caudal fin. Scales thin and cycloid, with fine concentric striations.

The generic name *Pholidolepis* is a composite one derived from *Pholidophorus* and *Leptolepis*, so as to indicate the probable intermediate position of the new genus between the two other genera.

Type species. Pholidolepis dorsetensis sp. nov.

Pholidolepis dorsetensis gen. et sp. nov.

(Pl. 7; Text-figs. 7, 8)

1895 Pholidophorus caudalis Woodward : 458 (partim).

PRELIMINARY DIAGNOSIS. *Pholidolepis* of rather small size, up to about 110 mm. in total length. Body elongate, depth about one-fifth of the length without caudal (standard length). Head less than one quarter of standard length. Preopercular sensory canal with about 15 tubules.

HOLOTYPE. British Museum (Nat. Hist.) No. 38164.

MATERIAL. In addition to the holotype, Nos. 35725, 38536, P.3662, P.44708, P.44709 of the British Museum (Natural History) and P.259, of the D.M.S. Watson Collection, Cambridge, have been used for the following description, all more or less badly preserved.

Besides these specimens there is, however, in the British Museum (Natural History) a number of still more defective specimens, probably belonging to *Ph. dorsetensis*: Nos. 35562, 38537, 39862, 43007, P.939, P939b, P.939c, P.4370, and P.44707.

DESCRIPTION. The holotype has a total length of about 110 mm.; length from tip of snout to posterior margins of hypurals (standard length) about 95 mm. Specimen P.44708 has a standard length of about 98 mm., P.3662 of about 80 mm., which lengths constitute the range for the specimens investigated.

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The body is decidedly more elongate than in *Ph. caudalis*, to which species the specimens in question have been referred by Woodward, but as all specimens are crushed the true depth of the body cannot be given with accuracy; it may be estimated as about one-fifth of the standard length. The length of the skull seems to be less than one quarter of the standard length.

The dermal bones of the head are comparatively thin ; as far as can be seen only the bones of the jaws show a surface ornamentation.

Exoskeletal skull roof

Only very little can be made out regarding the bones belonging to the exoskeletal skull roof because of the bad state of preservation.

The *premaxillary* is not visible in any of the specimens investigated.

The *rostral* may be present in Watson Colln. No. P.259, but only in a defective state.

The *nasal* (*Na*, Pl. 7, fig. 3; Text-figs. 7, 8) is rather well preserved in the holotype. It is an elongate, comparatively large bone reminiscent of the corresponding bone in *Ph. bechei* and situated lateral to the foremost part of the lateral margin of the frontal;



Ang, angular; De. Spl, dentary; Fr, frontal; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pop, preoperculum; Smx_1 , Smx_2 , anterior and posterior supra-maxillaries; Sop, suboperculum; poc, preopercular sensory canal; soc, supraorbital sensory canal.



anteriorly it is rounded and reaches about as far forwards as the anterior tip of the frontal. Its lateral outline cannot, however, be determined exactly because of damage and consequently it is impossible to say whether a notch or fenestra for the posterior nostril is present as in *Ph. bechei*.

The frontal (Fr, Pl. 7, figs. 1, 3; Text-figs. 7, 8) is preserved in the holotype, in 38536 and in Watson Colln. No. P.259, but in all these specimens it is more or less defective because of crushing. Its anterior half is, judging from the holotype, rather broad but tapers towards the anterior rounded tip at the level of the nasal. The posterior half broadens considerably but its posterior margin cannot be accurately defined in any specimens. There are no traces of surface ornamentation on the frontal.

No supraorbitals can be seen clearly in any specimens but some small bone fragments lateral to the lateral margins of the frontal and nasal in the holotype (So, Pl. 7, fig. 3) may belong to an anterior supraorbital similar to that bone in Ph. bechei.

Only the sensory canal of the *dermosphenotic* seems to be present in the holotype, the rest of the bone is missing. In the other specimens investigated this bone is not visible.

The *parietal*, the *dermopterotic* and the *extrascapular* are, in all specimens, too damaged for description.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pl. 7, figs. I-3; Text-fig. 7) is more or less completely preserved in the holotype as well as in 38536 and P.44708, and Watson Colln. No. P.259, but in none of them is it undamaged and its anterior, antero-mesially directed tip is not visible. Its posteriorly directed, lateral part is, as usual, evenly curved with the convexity directed ventrally. Its lateral surface is provided with a weak ornamentation, consisting of more or less oblique striations as can be seen in the holotype and particularly in P.44708 (Pl. 7, fig. 2). In the latter the ventral border of the maxillary carries a dentition similar to that in *Leptolepis*.

The supramaxillaries are only visible in P.44708 and Watson Colln. No. P.259. The anterior one, supramaxillary I $(Smx_1, Pl. 7, fig. 2)$, is partly preserved in the first named specimen and seems to be much longer antero-posteriorly than the corresponding bone in *Pholidophorus*, thus more like that of *Leptolepis*, but as its anterior part is damaged its outline cannot be made out with accuracy. If there exists any surface ornamentation on supramaxillary I it must be only weakly developed. Supramaxillary 2 $(Smx_2, Pl. 7, fig. 2)$ is also best preserved in P.44708; its antero-dorsal process is decidedly more pronounced than in *Pholidophorus* but not nearly so long as in *Leptolepis*. The lateral surface of supramaxillary 2 carries a weak longitudinal striation somewhat recalling that in *Ph. latiusculus* but much weaker. Both supramaxillaries seem to overlap the dorsal margin of the maxillary but only to a small degree.

The bones of the infraorbital series as well as the suborbital are practically missing in all specimens.

The *preoperculum* (*Pop*, Pl. 7, figs. 1, 3; Text-fig. 7) is present in most specimens but in none is it undamaged. It is best preserved in 38536 and has the same general



FIG. 8. Pholidolepis dorsetensis gen. et sp. nov. Attempted restoration of head in dorsal view. $\times 6.3$. Lettering as in Fig. 7.

shape as in *Leptolepis*, the anterior margins of the dorsal and the antero-ventral limbs meeting to enclose an angle, but it has a deep notch on its posterior margin as in *Ph. bechei*. There is no process on its anterior margin at the angle as there is, for example, in *Leptolepis normandica*.

The operculum (Op, Text-fig. 7) is very damaged by crushing or is lacking in all specimens except Watson Colln. No. P.259. Judging from this specimen its general shape is about the same as in *Pholidophorus*.

The suboperculum (Sop, Text-fig. 7) is also only preserved in Watson Colln. No. P.259. It seems to be comparatively deep, and the process at its antero-dorsal corner is longer and more pointed than in *Ph. bechei*.

Only the posterior part of the *interoperculum* (*Iop*, Text-fig. 7) is exposed in the specimen just named and in 38536, and nothing can be said about its general shape.

Lower jaw

The lower jaw is partly visible in the holotype and in 38536 and P.44708, and Watson Colln. No. P.259. Its outline cannot be determined, but in all specimens mentioned the anterior part of the *dentary* (*De. Spl.*, Pl. 7, figs. I-3; Text-fig. 7) ascends rather gently as in *Pholidophorus*, not abruptly as in *Leptolepis*; from this it may be concluded that the general shape of the lower jaw is also almost as in *Pholidophorus*. The ridge separating the dental and the comparatively low splenial parts of the dentary is clearly visible. In specimen P.44708 (Pl. 7, fig. 2) the lateral

surface of the *angular* (Ang, Pl. 7, fig. 2) is provided with a surface ornamentation of thin longitudinal ridges or streaks similar to those on the maxillary.

A gular plate is not visible in any of the specimens investigated.

Sensory canal system of head

"'e sensory canal system of the head is only partly visible and the description must therefore be rather incomplete.

Fart of the *supraorbital sensory canal* (soc, Pl. 7, figs. 1, 3; Text-figs. 7, 8) can be seen in the holotype, in 38536 and in Watson Colln. No. P.259. In its foremost part, piercing the nasal bone, the canal is straight and continues straight backwards in the anterior, narrower part of the frontal. As the frontal broadens the canal bends laterally and then runs obliquely postero-mesially; its posterior part in the parietal cannot be followed. No tubules or pores can be observed with accuracy except in Watson Colln. No. P.259, where three postero-mesially directed tubules are given off from the mesial side just before and at the bend of the canal.

Almost nothing can be made out regarding the *infraorbital sensory canal*. In the holotype only a small part of a sensory canal is present, probably the canal in the dermosphenotic (Dsph, Pl. 7, fig. 3), with the backward bend of the main canal and the antero-dorsally directed tubule.

Cephalic division of main lateral line

The cephalic division of the main lateral line can only be followed in the preoperculum.

The preopercular sensory canal (poc, Pl. 7, fig. 3) and its tubules follow the same general pattern as in *Ph. bechei*, but the number of tubules is lower. In the ventral limb of the preoperculum there are in 38536 eleven tubules, obviously corresponding to the 13 ventrally situated tubules in *Ph. bechei*; the posterior ones are, as in that species, long, narrow and curved with the convexity anteriorly directed. Dorsal to these tubules there are four shorter tubules, corresponding to the five to six shorter tubules in *Ph. bechei*. The total number of tubules is thus 15 in this specimen; in the others investigated the preoperculum is too damaged to allow a count of the tubules, but as far as can be observed the general pattern is the same as that just described for 38536.

Exoskeletal shoulder girdle and squamation

Parts of the *cleithrum* are exposed in many of the specimens but in no case can it be studied in any detail. No other bones belonging to the exoskeletal shoulder-girdle can be identified.

The squamation consists of thin cycloid scales with delicate concentric striations.

The lateral line

No lateral line can be seen with certainty in any of the specimens available.

Axial skeleton and paired and unpaired fins

The *vertebral centra* are thin bony cylinders which are, however, crushed or displaced in all specimens investigated; their undamaged shape cannot be described nor can their number be determined with any degree of accuracy. The neural and haemal spines are comparatively long.

The fins are in part rather well preserved but in the dorsal and anal fins the lepidotrichia are poorly preserved. No fulcra can be observed on the pectoral, ventral, dorsal or anal fins, but with regard to the two last named fins this statement needs confirmation on better preserved material.

The *pectoral fin* has a rather high number of lepidotrichia ; in P.3662 and P.44709, and Watson Colln. No. P.259 I have counted 19 rays, in P.44708 20 rays.

In the ventral fin the number of lepidotrichia is also rather high; in P.44708 and P.44709 and Watson Colln. No. P.259 their number is 15 or about as in *Ph. bechei.*

The *dorsal fin* is poorly preserved in all specimens, but in P.44709 the number of dorsal radials can be determined as 12, the anterior one as usual being composed of two elements.

The anal fin has 8 radials in the holotype and in 38536 and P.44709.

The *caudal fin* carries along its dorsal margin rather long and stout fulcra; no fulcra have been observed on the ventral margin of the fin.

REMARKS. There is no doubt that the specimens just described were erroneously identified as *Pholidophorus caudalis* Woodward, as can be seen from a comparison with the following description (see p. 411), and I have been unable to find another described species to which they can be referred. Consequently I have assigned them to a new species for which I propose the name *Pholidolepis dorsetensis*. Unfortunately the material on which the new species is based is rather defective, and I am not fully convinced that all specimens here referred to *Ph. dorsetensis* really belong to that species. In particular I am in doubt regarding Watson Colln. No. P.259, which shows very few details directly comparable with those exposed in the other specimens; it is especially unfortunate that almost nothing of the characteristic preoperculum is preserved. On the other hand I have not found any differences justifying its separation from the other specimens. More complete and better preserved material is necessary for a fuller description of *Ph. dorsetensis*.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.

Genus PHOLIDOPHOROIDES Woodward

1941 Pholidophoroides Woodward : 89.

EMENDED DIAGNOSIS. Pholidophoridae of medium size. Exoskeletal cranial bones and scales with ganoin covering. Nasal well developed and well separated from its antimere by the frontals, anteriorly reaching level of anterior margin of frontals. A single, well-developed supraorbital. Maxillary rather stout and deep with more or less pronounced convexity on dorsal margin ventral to infraorbital I (lachrymal) and supramaxillary I; posterior margin notched. Two supramaxillaries, not markedly overlapping dorsal margin of maxillary, supramaxillary 2 without marked process at antero-dorsal corner. Antorbital well developed, more than five (seven?) infraorbitals. Preoperculum with preopercular sensory canal running along middle of bone, about equidistant from anterior and posterior margins. Lower jaw not markedly deep, greatest depth in posterior third of its length ; dentary with smooth dental part, separated from splenial part by strong ridge. Dorsal fin above interspace between ventral and anal fins. Fulcra present along anterior margin of paired as well as unpaired fins. Caudal fin hemi-heterocercal with dorsal and ventral margins fulcrated. Scales moderately thick ; some longitudinal series of flank-scales higher than broad.

TYPE SPECIES. Pholidophoroides crenulata (Egerton).

REMARKS. When creating the new genus *Pholidophoroides* Woodward (1941:89) diagnosed it in the following manner: "One species from the Lower Lias, *P. crenulatus* Egerton, is distinguished from *Pholidophorus* by its smaller scales, which are less deepened on the flank. The scales are arranged in from 50 to 60 transverse rows, and those of the anterior part of the lateral line are less than twice as deep as broad. The scales are also comparatively thin, often displaying their concentric lines of growth. The fins are small like those of *Pholidophorus*. The maxilla seems to be comparatively stout. Ring vertebrae are conspicuous in the abdominal region.

P. crenulatus may therefore be regarded as the type-species of a distinct genus, *Pholidophoroides...* The Lower Liassic species, *P. caudalis* A. S. Woodw., probably also belongs to *Pholidophoroides.*"

The diagnosis given above is mainly based on the taxonomic characteristics of the redescribed type species, but also taking into consideration the other species here ascribed to the genus *Pholidophoroides*.

Pholidophoroides crenulata (Egerton)

(Pls. 8, 9, 10; Pl. 15, figs. 3, 4, 5, 8; Text-figs. 9-11)

- 1843 Pholidophorus crenulatus Egerton : 184.
- 1852 Pholidophorus crenulatus Egerton; Egerton, pl. 5.
- 1887 Isopholis crenulatus (Egerton) Zittel: 216.
- 1890 Pholidophorus crenulatus Egerton ; Woodward & Sherborn : 146.
- 1895 Pholidophorus crenulatus Egerton ; Woodward : 463, pl. 12, fig. 6.

1941 Pholidophoroides crenulatus (Egerton) Woodward : 89.

DIAGNOSIS. Pholidophoroides of medium size, at least up to 150 mm. in total length. Greatest depth of the body about one quarter of the standard length or slightly more (ca. 25-30% of that length). Depth of the caudal peduncle less than one-tenth (ca. 8-9%) of the standard length. Maxillary deep. Preopercular sensory canal with 16 or 17 tubules. Scales rather thin, in about 45-50 transverse rows reckoned from the hind margin of operculum to the middle of the caudal fin ; about four longitudinal rows of body scales somewhat deeper than broad and with the hind margin crenulated.

LECTOTYPE. British Museum (Natural History) Nos. P.572 and P.573 are the two specimens originally described and figured by Egerton (1843, 1852) and designated

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as "The two type specimens" by Woodward (1895:463). P.573 is the more complete specimen (standard length about 82 mm., height of body about 21 mm., height of caudal peduncle 7.5 mm.) and is therefore selected as lectotype.

MATERIAL. In addition to the lectotype, the specimens mainly used for the following description are P.153, P.421, P.572, P.1046*a*, *b*, P.4415, 38110, 38739, 38738; they agree in all comparable features with P.573.

DESCRIPTION. The total length of the largest specimen, P.1046*a*, is 150 mm.; its length from the tip of the snout to the hindmost scale in the lateral line (standard length) is about 125 mm. The other specimens in the British Museum (Natural History) have a standard length from 120 to 74 mm. The greatest depth of the body is about one quarter of the standard length or slightly more (*ca.* 25–30% of this length); the depth of the caudal peduncle is somewhat less than one-tenth (8–9%) of the standard length. The length of the head is about one quarter of the standard length, generally slightly less (*ca.* 22–25%).

The ventral fins are situated approximately midway between the tip of the snout and the hindmost lateral line scale and the distance between the base of the ventrals and the origin of the anal is about 75-85% of the distance between the bases of the pectoral and ventral fins.

A good figure of the entire fish is given by Woodward (1895, pl. 12, fig. 6).

The specimens most thoroughly investigated are rather well preserved with the bones of the skull exposed to a great extent, and consequently they allow the following description to be made.

Exoskeletal skull roof

The premaxillary (Pmx, Pl. 10, figs. 1, 2; Text-fig. 9) is visible in P.1046a, b, and to some extent also in P.4415 and 38738. It is comparatively stout with the postero-dorsal margin weakly S-shaped. The straight antero-ventral margin is serrated, forming a single row of teeth. The lateral surface of the premaxillary is densely set with ganoin tuberculations.

The rostral (Ro, Pl. 9; Text-figs. 9, 10) is best preserved in 38110, but cannot be studied in any detail. The part pierced by the ethmoidal commissure is a little swollen dorsally; posteriorly its lateral parts are concave and rather thin at the margin.

The *nasal* (*Na*, Pls. 8, 9; Text-figs. 9, 10) is also best exposed in 38110. It is an oblong, rather broad bone, situated posterior to the lateral parts of the rostral. It is, on the whole, oval but its antero-lateral and postero-lateral margins (lateral to the posterior opening for the supraorbital sensory canal) are concave, probably marking the postero-mesial and antero-mesial limits of the anterior and posterior nasal openings respectively. The nasals are separated by the narrow anterior part of the frontals.

The *frontal* (Fr, Pls. 8, 9; Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) is rather narrow in its anterior part, mesial to the nasal, but it broadens considerably posterior to the nasal; from there its lateral margin runs at first almost straight posteriorly, but behind the orbit the bone widens again and has its greatest breadth in its posterior



FIG. 9. Pholidophoroides crenulata (Egerton). Attempted restoration of head in lateral view. $\times 5$ approx.

Ang, angular; Ant, antorbital; De. Spl, dentary; Dpt, dermopterotic; Dsph, dermosphenotic; Ext, extrascapular; Fr, frontal; Ifo_1 - Ifo_7 , infraorbitals I to 7; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pa, parietal; Pmx, premaxillary; Pop, preoperculum; Ro, rostral; Sbo, suborbital; "Sbo", "accessory suborbital"; Scl, supracleithrum; Smx₁, Smx₂, anterior and posterior supramaxillaries; So, supraorbital; Sop, suboperculum; Ssc, suprascapula; ant. br, antorbital branch of infraorbital sensory canal; ap, anterior pit-line; ifc, infraorbital sensory canal; ifc. com, ethmoidal commissure; mdc, mandibular sensory canal; mp, middle pit-line; poc. preopercular sensory canal; pp, posterior pit-line; s. com, supratemporal commissure; soc, supraorbital sensory canal.

part. Its postero-lateral corner is rounded off and its posterior margin is irregularly wavy. The suture between the frontals is practically straight anteriorly ; posteriorly its course is difficult to follow, but it does not seem to be markedly sinuous.

A strong *supraorbital* (So, Pl. 9; Text-figs. 9, 10) is situated behind the posterior nasal opening and lateral to the broadened part of the frontal posterior to the nasal. Anteriorly its dorsal surface bulges a little and is ornamented with some small elevations. In dorsal aspect the lateral border of the supraorbital is almost straight, ending anteriorly in a point.

A very small bone between the lateral margin of the frontal and the anterior tip of the dermosphenotic in 38739 (So?, Pl. 8; Pl. 15, fig. 4) may perhaps be a small second supraorbital; in P.1046b a similar small bone may be traced, but as I have

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not found a corresponding element in any of the other specimens investigated, it may perhaps be only a fragment of the anterior part of the dermosphenotic or of the lateral frontal margin.

The dermosphenotic (Dsph, Pls. 8, 9; Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) is mostly more or less crushed on the underlying autosphenotic. Its anterior part, situated along the postero-lateral margin of the frontal, is pointed and a little curved and constitutes the postero-dorsal border of the orbit. Its posterior margin cannot be determined with accuracy, but according to P.1046b it seems to be rounded off.

The margins of the *parietal* (*Pa*, Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) are difficult to determine, as the skull roof of the single specimen showing the cranial bones in dorsal view, 38110, is much crushed in its posterior part, but judging from 38730 it has a rather wide extension laterally, thus being much broader than long.

The *dermopterotic* (*Dpt*, Pls. 8, 9; Pl. 10, fig. 2; Pl. 15, fig. 4; Text-figs. 9, 10) is comparatively narrow in its anterior part between the frontal and the dermosphenotic but broadens continuously backwards, attaining its greatest breadth at its straight posterior margin.

The shape of the *extrascapular* (*Ext*, Pl. 9; Pl. 10, fig. 2; Text-figs. 9, 10) cannot be determined; its lateral part is, however, almost triangular with the posterolateral margin a little convex and the postero-mesial margin slightly concave. The mesial part of the extrascapular is not preserved in any of the specimens investigated.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9) is strikingly large and stout. Its anterior, mesially directed part is only partly visible in the specimens investigated, but seems to be rather low; its dorsal margin has an arched, thickened edge with the convexity directed ventrally, fitting the concavity on the postero-dorsal margin of the premaxillary; the surface covered by the premaxillary is smooth. The lateral, posteriorly directed part of the maxillary increases rapidly in height; its ventral margin is evenly convex, but its dorsal margin, on the whole concave, has a marked convexity below infraorbital I and supramaxillary I. The posterior margin of the maxillary is rather deeply notched. The anterior half of the lateral surface has, nearest to the premaxillary, an ornamentation of densely set tuberculations like those on the premaxillary; posteriorly the ornamentation becomes a longitudinal striation parallel to the margins. The posterior half of the lateral margin is smooth except for some longitudinal striations along the dorsal margin; in P.4415 there are, also, some longitudinal ganoin streaks parallel to the ventral margin. A delicate comb-like dentition, about as in Leptolepis, is present along the posterior half of the ventral margin, the teeth decreasing in length anteriorly. No teeth can be observed along the anterior half of the ventral margin, but whether this is the actual condition or only dependent upon the state of preservation, must remain undecided.

Two supramaxillaries are situated dorsal to the maxillary, not markedly overlapping its dorsal margin. The anterior one, supramaxillary I (Smx₁, Pls. 8, 9; Pl. 10, figs. I, 2; Text-fig. 9), is rather small, almost semicircular, and has a well-



FIG. 10. Pholidophoroides crenulata (Egerton). Attempted restoration of head in dorsal view, the snout flattened, with (right) the probable mutual positions of the bones of the snout. $\times 5$ approx. Lettering as in Fig. 9.

marked concentric striation on its lateral surface. The posterior one, supramaxillary 2 (Smx_2 , Pl. 8; Pl. 10, figs. 1, 2; Text-fig. 9), is considerably larger; its anterior margin is concave, fitting the convexity of supramaxillary 1, but its antero-dorsal corner is not markedly produced into a process. The dorsal and ventral margins of supramaxillary 2 are evenly convergent towards the posterior tip of the bone. Supramaxillary 2 also has a well-marked concentric striation on its lateral surface.

The bones of the infraorbital series are generally well preserved, only infraorbital 2 is lacking in all specimens investigated.

The antorbital (Ant, Pls. 8, 9; Pl. 10, fig. 2; Text-figs. 9, 10) is an almost \bot -shaped bone situated ventro-lateral to the rostral and the nasal; its posterior tip reaches the antero-lateral tip of the supraorbital.

Ventral to the antorbital and between it and the anterior part of the maxillary and supramaxillary I there is a large *infraorbital* I or *lachrymal* (*Ifo*₁, Pl. 8; Pl. 10, figs. I, 2; Text-fig. 9). Its anterior margin is semicircular and its ventral margin is slightly convex; its dorsal margin is not clearly visible but is probably slightly concave.

Infraorbital 3 (Ifo₃, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9) is comparatively large, stretching from the orbit to the anterior margin of the preoperculum; its anteroventral margin is slightly concave.

The following bones in the series, dorsal to infraorbital 3, are crushed, displaced or lacking in most specimens, but judging from 38110 and P.1046a and b there are about four small, square infraorbitals between infraorbital 3 and the dermosphenotic $(Ifo_4, Ifo_5, Ifo_6, Ifo_7, Pl. 9; Text-figs. 9, 11)$; in 38110 there seems to exist one more element in the series on the right side $(Ifo_8?, Pl. 9; Text-fig. 11)$, but here the arrangement is rather obscure.



FIG. 11. Pholidophoroides crenulata (Egerton). Infraorbital 3, postorbital infraorbitals and suborbitals (same specimen as on Pl. 9). Lettering as in Fig. 9; A right side, B left side. B.M. $_{38110.}$ $\times 5$ approx.

A large suborbital (Sbo, Pls. 8, 9; Pl. 10, fig. 2; Text-fig. 9) bone is situated posterior to infraorbitals 4-7, covering the hyomandibular; as a rule it is crushed in the middle on to the strong lateral crest of this latter bone. Dorsal to the suborbital there are in 38110 ("Sbo", Pl. 9; Text-figs. 9, 11) two small bones on the right side and a single similar bone on the left side, tapering posteriorly and, like the suborbital, with a conspicuous concentric surface striation. A single similar bone is also seen in 38738. It is difficult to interpret these bones; they may be homologous to the supraspiracular plates described by Stensiö (1932, text-fig. 67) in Perleidus stoschiensis Stensiö and by Lehman (1952, text-figs. 85, 86) in P. madagascariensis But they are more likely to be "accessory suborbitals". In many Piveteau. holosteans there is a series of suborbitals posterior to the infraorbitals which may fuse or remain separate in various ways. Thus, for example the posterior part of infraorbital 3 in Pholidophoroides as well as in Leptolepis is probably the originally ventralmost suborbital, secondarily fused with infraorbital 3 (cf. Stensiö 1947: 164), whereas the others as a rule fuse into a single, large suborbital. In Ph. crenulata the dorsalmost component or components may remain free, at least in some specimens.

The peculiar condition of the dorsalmost infraorbitals and the "accessory suborbitals" on the right side in 38110 is also difficult to interpret. It may be due to an ontogenetic disturbance or perhaps to regeneration after an injury. The *preoperculum* (*Pop*, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9) is a weakly crescentic bone with a dorsal, more or less vertical limb and an antero-ventrally directed ventral limb, much broader than the dorsal one. Its posterior margin has, ventral to the more or less pronounced angle between the two limbs, a characteristic shallow concavity or indentation.

The operculum (Op, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9) is roughly triangular; its anterior, vertical margin and its postero-ventral margin are straight and its dorsal margin rounded off. The anterior margin is thickened ventral to the facet for the processus opercularis of the hyomandibular.

The suboperculum (Sop, Pls. 8, 9; Pl. 10, figs. 1, 2; Text-fig. 9) is comparatively large and its antero-dorsal process anterior to the ventral tip of the operculum is remarkably broad and strong. According to 38739, P.1046b and P.4415 the posterior margin of the suboperculum has dorsally a shallow concavity or indentation.

The *interoperculum* (*Iop*, Pl. 8; Pl. 10, figs. 1, 2; Text-fig. 9) has a roughly triangular shape, with the posterior and ventral margins a little concave.

Branchiostegal rays and gular plate

There seems to be a rather large number of *branchiostegal rays*; they are best exposed in P.4415 (R. Br, Pl. 10, fig. 1), on which 16 rays can be seen, but more small ones may exist in front of the anteriormost of the exposed rays.

P.1046b shows parts of a rather large median gular plate (Gu, Pl. 10, fig. 2). Its anterior tip is a little bent upwards, but as the lateral margin is broken off, nothing can be stated regarding its shape.

Lower jaw

The lower jaw is generally only partly exposed, its dorsal margin being covered by other bones in all specimens investigated except in P.153 (Pl. 15, fig. 5), where the lower jaw is isolated and its outline can be determined rather exactly; its greatest depth is somewhat less than half of its length.

The ventral, splenial part of the *dentary* (*De. Spl*, Pl. 8; Pl. 10, figs. 1, 2; Pl. 15, fig. 5; Text-fig. 9) is limited dorsally by a well-marked ridge, and its lateral surface is ornamented with longitudinal ganoin striations and rugosities. The dental part is only gently ascending anteriorly and its lateral, slightly convex surface is not ornamented. In P.153 a few very small teeth can be observed on its margin. Approximately between the first and second third of the length of the lower jaw the dental part ascends abruptly and is thickened; this thickening obviously corresponds to the dorsally directed thickening of the dentary in *Leptolepis*.

Only the ventral part of the *angular* (or more precisely *angulo-supra-angular*, though no limit between the two components can be determined) is generally exposed (Ang, Pl. 8; Pl. 10, figs. 1, 2); in P.153 (Ang, Pl. 15, fig. 5) it is, however, entirely exposed although partly crushed and defective. Because of this it is not possible to determine its anterior margin in the dorsal part; anteriorly it is rounded. Postero-ventrally the lower jaw ends in a conical point, reminiscent of a dermarticular.

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but as no suture can be seen separating it from the rest of the angular, it must be only the hindmost part of that bone. The postero-ventral part of the lateral surface of the angular, obviously exposed when the mouth is closed, is ornamented with ganoin streaks and small tuberculations, for the rest the lateral surface of the bone is smooth.

In P.4415 the hindmost part of the right lower jaw is exposed in medial view, showing the *articular* (*Art*, Pl. 10, fig. 1; Pl. 15, fig. 8) with its articular fossa for the quadrate and a small but well marked ossified processus coronoideus.

No true dermarticular has been observed.

Sensory canal system of head

The sensory canal system of the head is well developed as canals embedded in the bone tissue with short tubules and pores.

The supraorbital sensory canal (soc, Pl. 9; Pl. 15, fig. 3; Text-figs. 9, 10) pierces the nasal, the frontal and the parietal. The following description is based on 38110.

In the nasal the canal describes an arch from near the anterior end of the lateral margin to near the mid-line of the bone and then passes almost straight back to the posterior tip of the nasal. At the bend it possesses an elevated, rather large pore, and further back there are two more pores or short tubules. There is no evidence of a communication between the supraorbital and the infraorbital sensory canals.

From the nasal the canal passes over into the frontal at its concave margin behind the nasal, running at first almost straight backwards and then curving in a posterolateral direction parallel to the lateral margin of the frontal before continuing posteromedially to the posterior margin of the bone. The number of tubules issuing from the frontal part of the canal seems to vary a little on both sides. On the dorsal side of the anterior straight part of the right canal there is a small pore, and further posteriorly a short tubule seems to issue from the lateral side ; where the canal bends it gives off a mesial series of 9 tubules of various lengths, and further backwards there seem to be two more, posteriorly directed tubules. On the left side a conspicuous tubule issues from the lateral side of the anterior straight part of the canal (a corresponding tubule is seen also in 38738); more posteriorly the canal gives off at least 7 postero-mesially directed tubules and at least one posteriorly directed tubule; a short distance anterior to the posterior margin of the frontal there is a conspicuous pore on the dorsal surface of the canal.

The parietal contains only a very short part of the supraorbital sensory canal without pores or tubules, ending as a short groove which represents the anterior pit-line.

The *infraorbital sensory canal (ifc*, Text-figs. 9, 11) begins with a slightly arched ethmoidal commissure in the rostral, joining the canals of both sides; no pores or tubules belonging to the ethmoidal commissure can be observed.

From the rostral the canal passes over into the antorbital and pierces its anterior broader part, sending out posteriorly an antorbital branch. The antorbital part of the sensory canal system possesses four dorsal pores of which two are on the main

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canal, one on its mesial part and one about dorsal to the point where the antorbital branch comes off, and one is in the anterior and one in the posterior part of this branch.

From the antorbital the infraorbital sensory canal passes over into infraorbital I (lachrymal) and runs parallel to the anterior and ventral margins of this bone. From its anterior, arched part the canal sends out two very short, forwardly directed tubules, sometimes looking like wide pores, and from the ventral side there issue about 7 postero-ventrally directed tubules.

As infraorbital 2 is missing in all specimens available, nothing can be said about the part of the canal belonging to this bone.

In infraorbital 3 the number of tubules seems to be subject to rather great individual variation. In P.1046b (Pl. 10, fig. 2) the somewhat defective infraorbital 3 shows three large tubules, in P.421 and 41857 there are likewise three tubules and in 38110 there are three large, well separated tubules, whereas in P.1046*a* and 38738 four tubules are situated rather close together; in 38739 there are two groups each of three small tubules.

In the remaining small infraorbitals the sensory canal seems to give off a single, posteriorly directed tubule in each bone.

Regarding the course of the infraorbital sensory canal in the dermosphenotic nothing can be stated with accuracy because of the defective state of preservation of this bone.

In the dermopterotic the sensory canal runs along the lateral margin of the bone. Dorsally it gives off four short tubules. To what extent this canal belongs to the sensory canal system of the head and to the cephalic division of the main lateral line, respectively, is a question which must be left open. The point at which it gives off the preopercular sensory canal cannot be determined.

Cephalic division of main lateral line

On the posterior part of the parietal there is a transverse, slightly arched groove with its convexity directed postero-mesially; this groove may represent the middle pit-line (m.p, Pl. 15, fig. 3; Text-fig. 10). A groove mesial to it may be the posterior pit-line (pp, Pl. 15, fig. 3; Text-fig. 10).

The cephalic division of the main lateral line passes over from the dermopterotic into the extrascapular and continues backwards to the suprascapular, giving off mesially the supratemporal commissure (s. com, Text-figs. 9, 10), but the course of these canals cannot be followed exactly. Judging from the fragmentary extrascapular on the left side in 38110 (Pl. 9) the main canal gives off laterally a large tubule, and at least four tubules are given off posteriorly from the lateral part of the supratemporal commissure; its mesial part is missing. In the fragmentary right extrascapular of the same specimen there seem to be two tubules given off laterally from the main canal; the supratemporal commissure and its tubules are lacking. The *preopercular sensory canal* (Text-fig. 9) pierces the preoperculum in the middle

The *preopercular sensory canal* (Text-fig. 9) pierces the preoperculum in the middle of its length almost parallel to its anterior and posterior margins. In 38739 (Pl. 8) it gives off posteriorly 17 tubules, almost evenly distributed over the whole length

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of the canal, five of which are situated in the dorsal limb of the bone, dorsal to the obtuse posterior angle, but as the antero-ventral tip is not entirely exposed it is possible that one more tubule ought to be added to this number. In P.1046b (Pl. 10, fig. 2) there are likewise 17 tubules, four of which are situated in the dorsal limb, but between tubules 7 and 8 reckoned from the antero-ventral tip of the bone there is in addition a short tubule, probably only a branch of tubule 7; tubules I-7 are situated close together. Specimen 48009 also shows I7 tubules issuing from the morphologically posterior side of the preopercular sensory canal, whereas in P.421 and P.3595 only I5-I6 tubules could be determined with accuracy. In 38738 five tubules are clearly visible in the dorsal limb of the preoperculum.

In P.1046b and P.4415 the lateral surface of the preoperculum possesses a wellmarked groove which may be the posterior portion of the anterior division of the supramaxillary pit-line (hc_1 , Pl. 10, figs. 1, 2). A postmaxillary pit-line cannot be traced in any of the specimens investigated except in P.421; in this specimen the middle of the lateral surface of the preoperculum shows a vertical groove which I interpret as the postmaxillary pit-line.

The mandibular sensory canal (mdc, Text-fig. 9) cannot be followed because of the thickness of the splenial part of the dentary, but in P.1046b (Pl. 10, fig. 2) many of its short, backwardly directed tubules are discernible, their openings being accentuated by ganoin thickenings.

On the lateral surface of the angular there is postero-ventrally a short vertical groove in P.153 and P.4415 which must be the oral pit-line $(orp_1, Pl. 10, fig. 1; Pl. 15, figs. 5, 8)$.

Exoskeletal shoulder girdle and squamation

Very little can be said about the *suprascapula* and the *supracleithrum*, which are only fragmentarily preserved in 38110 (*Ssc*, *Scl*, Pl. 9) and almost entirely destroyed by crushing in the other specimens investigated ; the outline of the suprascapula and the supracleithrum as given in the attempted restoration (*Ssc*, *Scl*, Text-fig. 9) is consequently very doubtful.

The *cleithrum* and the *postcleithrum* are not sufficiently exposed in the specimens available to allow their description in any detail.

The *scales* are arranged in about 45–50 transverse rows reckoned from the hind margin of the operculum to the middle of the caudal fin; posterior to the last row there are about 8–9 rows on the body axis dorsal to the lateral line, thus in all about 55–60 rows, which accords well with Woodward's (1941) statement of about 50–60 transverse rows. On the body there are generally four, sometimes only three, longitudinal rows of enlarged scales, the deepest being about twice as deep as broad and with the posterior margin crenulated; the number of points on the posterior margin is about 8, seldom up to 10 on the largest scales, but it decreases posteriorly in accordance with the decreasing depth of the scales.

The scales are comparatively thick on the middle and posterior parts of the body as well as on the tail; on the anterior part of the body they are, however, thinner and show, as stated by Woodward, a concentric striation. In most specimens investigated this striation is visible only in a few transverse rows behind the skull; in P.1046b, however (Pl. 10, fig. 2), such thin striated scales cover the whole anterior part of the body and extend posteriorly almost to the level of the pelvic fin base.

Lateral line

The lateral line pierces the suprascapula, and seems to give off three short but rather wide, mesially to postero-mesially directed tubules. In the supracleithrum the course of the sensory line is not clearly visible in any of the specimens available, but it seems to give off three postero-mesially directed tubules.

The anterior lateral line scales are rather indistinct, but more posteriorly they are clearly visible, each scale having a distinct pore on its lateral surface. The course of the lateral line is almost straight, along the middle of the body, ending at the base of the middle caudal lepidotrichia.

Axial skeleton and paired and unpaired fins

The *axial skeleton* consists of rather thin ring-vertebrae, which are partly visible in some of the specimens available; in none of them, however, are the vertebrae exposed to such a degree that anything can be made out regarding their shape and number.

The *pectoral fin* is of moderate size. The number of lepidotrichia is rather high; in P.4415 not less than 26 lepidotrichia can be counted, the ventralmost ones are, however, very small and articulated almost from their bases. In the type specimens P.572 and P.573 as well as in P.1046b and 47461 there seem to be at least 23 or 24 lepidotrichia. The first lepidotrichium is strong and rather densely set with fulcra (Fu, Pl. 8).

In the ventral fin the number of lepidotrichia amounts to 15, which number I have counted in P.1046b and P.4415. As in the pectoral fin the last two or three lepidotrichia are rather delicate and easily overlooked. The first two lepidotrichia are rather short and unarticulated, the third one (the first branched lepidotrichium) is densely set with small fulcra. Lateral to the base of the ventral fin there is a large axillary scale and enlarged scales also occur between the fins of both sides.

The dorsal fin has, anteriorly, two unarticulated lepidotrichia, the first as a rule rather short, the second longer. The third, long lepidotrichium carries a series of small fulcra on its anterior margin. The total number of lepidotrichia is difficult to determine as in most specimens the last rays are covered by scales or are defective; in P.1046*a* there are, however, about 14–15 lepidotrichia, and in P.421 I have counted 15. The number of dorsal radials cannot be stated because of the thickness of the squamation.

The anal fin has, as in the dorsal fin, two unarticulated lepidotrichia anteriorly followed by a third long, fulcrated lepidotrichium; the total number of lepidotrichia is difficult to determine but seems to be at least II-I2. No anal radials are visible.

The *caudal fin* may be interpreted as hemi-heterocercal, the scaled lobe dorsal to the lateral line (the reduced body axis) reaching farther posteriorly than the scaled ventral lobe. The dorsal and ventral margins are densely set with small fulcra.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.

Pholidophoroides limbata (Agassiz)

(Pls. 11, 12; Text-fig. 12)

1833 Pholidophorus limbatus Agassiz, 2, 1:9.

1843 Pholidophorus limbatus Agassiz, 2, pl. 37, figs. 1-5.

1844 Pholidophorus limbatus Agassiz, 2, 1:282.

1895 Pholidophorus limbatus Agassiz; (partim) Woodward: 464, pl. 12, fig. 7.

DIAGNOSIS. Pholidophoroides similar to Ph. crenulata but somewhat larger in size, at least up to 180 mm. in total length. Greatest depth of body nearly one-third of standard length or slightly less (ca. 28-32% of that length). Depth of caudal peduncle one-tenth of standard length or slightly more (10-11%). Maxillary proportionately not quite as deep as in Ph. crenulata. Preopercular sensory canal with about 14 tubules. Scales rather thick in about 40-42 transverse rows reckoned from hind margin of operculum to middle of caudal fin; five to six longitudinal rows of body scales deeper than broad with hind margin strongly though finely serrated.

HOLOTYPE. Unknown. Agassiz says (loc. cit., p. 283): "Il en existe des exemplaires dans plusieurs collections d'Angleterre, entre autres au Musée d'Oxford, dans les collections de lord Enniskillen et de sir Philipp Egerton." None of the specimens from the two last named collections [now in the British Museum (Natural History)] agree with either of the figures (pl. 37, figs. 1, 2) given by Agassiz. I have had no opportunity to visit the Oxford Museum collection. Woodward (1895) remarks : "Type. Distorted specimens of trunk", but gives no information regarding the collection to which they belong. P.1047 is chosen as LECTOTYPE.

MATERIAL. The following description is based mainly on P.1047, P.1047*a*, P.3596, P.4422, 36472, 38531, and 41906. Specimens P.1047*b* and *c*, P.3632, 38532 and 27595 also belong to this species but are more defective, and from them only little could be added to the description; P.4410 is perhaps not referable to *Ph. limbata*. P.7582, an "imperfect skeleton probably of this species" according to Woodward (1895: 466) belongs to the species described below (p. 416) as *Pholidophoropsis maculata* sp. n.

DESCRIPTION. The total length of the largest specimen, P.1047, is 180 mm., its length from the tip of the snout to the hindmost lateral line scale (standard length) is estimated at 150 mm. The other specimens have a standard length varying between about 140 and 108 mm. The greatest depth of the body is nearly one-third of the standard length or slightly less (about 28-32%), the depth of the caudal peduncle is about 10-11% of the standard length; the depth of the body and of the

caudal peduncle are consequently somewhat greater in this species than in *Ph. crenulata*. The length of the head is about one quarter of the standard length or slightly less (about 23-25%), about the same as in the type species.

The ventral fins are situated approximately midway between the tip of the snout and the hindmost lateral line scale, and the distance between the base of the ventrals and the origin of the anal is about 78-88% of the distance between the bases of the pectoral and ventral fins, about as in *Ph. crenulata*.

A good figure of the entire fish is given by Woodward (1895, pl. 12, fig. 7).

All specimens available are unfortunately more or less defective with respect to the snout region and the skull roof, consequently the following description of the cranial bones is rather incomplete and provisional. Presumably it will, however, be sufficient to demonstrate the close relationship between *Ph. limbata* and the type species of the genus.

Exoskeletal skull roof

This part of the skull is more or less defective in the specimens available. In specimen P.1047 nothing of it is preserved, in 38531 only the dermosphenotic, the dermopterotic and the extrascapular are partly present, in P.4422 and 36472 some bones of the snout region can be observed, but they are partly defective and dislocated.

The premaxillary (Pmx, Pl. 12, figs. 1, 2; Text-fig. 12) is rather well exposed, after preparation, in P.4422. It is an almost square, slightly tunid bone with the lateral surface almost smooth, not tuberculated as in Ph. crenulata. The anteroventral margin carries a single row of comparatively large teeth, considerably larger than in Ph. crenulata; they are slightly curved and increase in length posteriorly.

The *rostral* (*Ro*, Pl. 12, fig. 2; Text-fig. 12) is to a great extent visible in P.4422 as a thin, somewhat bulging bony plate, partly covering a bone which may be the mesethmoid.

The *nasal* is missing in P.4422, but in 36472 (*Na*, Pl. 11, fig. 2) there is an oblong bone, obviously pierced by a sensory canal, which I interpret as the right nasal. Its outline cannot, however, be determined in detail.

The *frontal* (*Fr*, Pl. 11, fig. 2; Text-fig. 12) is preserved, though much crushed and broken off anteriorly, in P.4422; in 36472, on the other hand, the anteriormost part of the frontal is preserved. Judging from these two specimens the frontal has on the whole the same shape as in *Ph. crenulata*.

Part of a *supraorbital* is present in P.4422, but it gives no information regarding the shape of this bone.

The *dermosphenotic* is missing or only present as fragments in all the specimens investigated; in 38531 (*Dsph*, Pl. 12, fig. 3) its anterior, pointed part is clearly visible, indicating that its shape is about the same as in *Ph. crenulata*.

The outline of the *parietal* is impossible to determine.

The *dermopterotic* (*Dpt*, Pl. 11, fig. 2; Pl. 12, fig. 3; Text-fig. 12) does not seem to differ in general from that of *Ph. crenulata*; parts of it are exposed in P.4422, 36472, and 38531.



FIG. 12. Pholidophoroides limbata (Agassiz). Attempted restoration of head in lateral view. $\times 4.2$.

Ang, angular; Ant, antorbital; De. Spl, dentary; Dpt, dermopterotic; Dsph, dermosphenotic; Ext, extrascapular; Fr, frontal; Ifo_1 - Ifo_7 , infraorbitals I to 7; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pa, parietal; Pmx, premaxillary; Pop, preoperculum; Ro, rostral; Sbo, suborbital; "Sbo", "accessory suborbital"; Smx₁, Smx₂, anterior and posterior supramaxillaries; So, supraorbital; Sop, suboperculum; ant. br, antorbital branch of infraorbital sensory canal; hc_1 , anterior division of supramaxillary pit-line; ifc, infraorbital sensory canal; ifc. com, ethmoidal commissure; orp, postmaxillary pit-line; orp₁, oral pit-line; poc, preopercular sensory canal; soc, supraorbital sensory canal.

The extrascapular (Ext, Pl. 12, fig. 3; Text-fig. 12) is as a rule very defective; in specimen 38531, however, its lateral part is well exposed, its antero-lateral corner being rounded and its postero-lateral and postero-mesial margins almost straight.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pl. II, figs. I, 2; Pl. I2, figs. I, 2; Text-fig. I2) is well preserved in P.1047 and 36472, its anterior, mesially directed part is, however, not entirely visible but seems to be rather low as in *Ph. crenulata*. The lateral, posteriorly directed part is not as deep as in *Ph. crenulata*, but otherwise both species agree closely in the most important characteristics, such as the convexity of the dorsal margin below infraorbital I and supramaxillary I, the deeply notched posterior margin and the longitudinal striation of its lateral surface. The posterior part of the convex ventral margin of the maxillary has, as in *Ph. crenulata*, a delicate, comb-like dentition, but anteriorly there is in P.4422 (Pl. 12, fig. I) a single row of small tuberculations, obviously the bases of somewhat larger teeth which have been broken off. The same arrangement can also be observed on the ventral margin of the left maxillary in 36472 (Mx_s , Pl. II, fig. 2).

The two supramaxillaries $(Smx_1, Smx_2, Pl. II, figs. I, 2; Text-fig. I2)$, only well preserved in P.I047 and 36472 (in the last named specimen partly pushed in below the dorsal margin of the maxillary), are also similar to those of *Ph. crenulata* with regard to shape and the presence of a well-marked striation on the lateral surface. The antero-dorsal corner of supramaxillary 2 does not seem to be drawn out into a larger process.

The bones of the infraorbital series are only partly preserved.

In specimens P.4422 and 36472 there is a defective bone in the snout region which may be interpreted as an *antorbital* (*Ant*, Pl. 11, fig. 2; Pl. 12, fig. 2; Text-fig. 12); its shape seems to be about as in *Ph. crenulata* but its outline cannot be determined exactly.

Infraorbital 1 (lachrymal) (If o_1 , Pl. 11, figs. 1, 2; Pl. 12, fig. 2; Text-fig. 12) is present only in P.1047, P.4422, and 36472, in all three specimens only as a fragment; however, from what can be observed it agrees with that of *Ph. crenulata*.

An *infraorbital* 2 (Text-fig. 12) is present in P.4422 ; it is elongate antero-posteriorly, its dorsal margin is slightly concave and its ventral margin correspondingly convex.

Infraorbital 3 (If o_3 , Pl. 11, figs. 1, 2; Pl. 12, fig. 3; Text-fig. 12) is present in P.1047, P.4422, 36472 and 38531. Its outline cannot be followed exactly in all specimens, but as compared with the corresponding bone in *Ph. crenulata* its posterior part seems to have a greater dorso-ventral extension.

Dorsal to infraorbital 3 there is in 38531 (Pl. 12, fig. 3) a well-preserved *infraorbital* 4, and further dorsally there seem to be traces of three more infraorbitals. In 36472 (Pl. 11, fig. 2) infraorbital 4 is partly exposed, infraorbital 5 is clearly visible and dorsal to it there are some fragments probably of two more infraorbitals. Consequently, as in *Ph. crenulata* there seem to be seven infraorbitals altogether.

The suborbital (Sbo, Pl. 11, figs. 1, 2; Pl. 12, fig. 3; Text-fig. 12) is partly preserved in P.1047, P.4422, 36472 and 38531. Corresponding to the comparatively great depth of infraorbital 3 in this species, the suborbital is not as deep as in *Ph. crenulata*. In both P.4422 and 36472 ("*Sbo*", Pl. 11, fig. 2; Text-fig. 12) a small bone, fragmentary in P.4422, has been observed between the suborbital and the dermopterotic, which probably corresponds to the "accessory suborbital" found in some specimens of *Ph. crenulata*.

The *preoperculum* (*Pop*, Pl. 11, figs. 1, 2; Pl. 12, fig. 3; Text-fig. 12) has, on the whole, the same shape as in *Ph. crenulata*, but it is somewhat straighter, the posterior margin being more evenly arched with only a little-marked angle between the dorsal

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and the ventral limbs and almost without the shallow concavity or indentation ventral to the angle that is found in *Ph. crenulata*.

The operculum, the suboperculum and the interoperculum seem not to differ in shape from the corresponding bones in *Ph. crenulata*.

Branchiostegal rays and gular plate

Some branchiostegal rays (R. Br, Pl. 11, fig. 1, Pl. 12, fig. 3) are preserved in P.1047 and 38531; they show nothing of special interest. A gular plate is not visible in any of the specimens investigated.

Lower jaw

The lower jaw is partly exposed in P.1047, P.4422 and 36472. The dental part of the dentary has a smooth lateral surface and the lateral surface of the splenial part of the bone is more or less ornamented with a longitudinal ganoin striation as in *Ph. crenulata*. No dentition can be observed with certainty.

Sensory canal system of head

Due to the fragmentary preservation of the skull very little can be said about the sensory canal system of the head.

In 36472 the anterior part of the *supraorbital sensory canal* is indicated in the nasal by an anterior and a posterior opening; because of the thickness of the bone the course of the canal between the two openings cannot be observed with accuracy. In P.4422 the hindmost part of the sensory canal in the frontal and its short continuation in the parietal may be traced. For the rest the supraorbital sensory canal and its tubules and pores cannot be seen.

Of the *infraorbital sensory canal*, only the following few remarks can be given. In P.4422 the ethmoidal commissure (*ifc. com*, Pl. 12, fig. 2; Text-fig. 12) joining the infraorbital sensory canals of both sides can clearly be seen as an arched bony tube which is slightly elevated above the dorsal surface of the rostral. Laterally there seem to be one or two pores, but whether they really are pores cannot be stated with certainty.

In the antorbital the infraorbital sensory canal seems to have about the same course as in *Ph. crenulata*, but because of the defective state of this bone a more detailed description cannot be given.

In infraorbital I (lachrymal), partly preserved in P.1047, the sensory canal has the same course along the anterior and ventral margins of the bone as in *Ph. crenulata*; of the tubules only the ventral one of the two pore-like tubules from the anterior, arched part of the canal and the three anterior tubules from the ventral part of the canal can be seen. In P.4422 and 36472 only a small part of the sensory canal is preserved.

In infraorbital 2 the sensory canal runs parallel to the dorsal and ventral margins of the bone. Whether this part of the canal gives off a tubule may be left open. In infraorbital 3 the sensory canal gives off, posteriorly, three rather long tubules in P.1047 (Pl. 11, fig. 1) and four tubules in 38531 (Pl. 12, fig. 3). In *Ph. limbata*, as in *Ph. crenulata*, the number and arrangement of the tubules in this bone are subject to individual variation. The canal and its tubules cannot be observed in P.4422 and 36472.

In infraorbital 4, clearly visible only in 38531 (Pl. 12, fig. 3), the canal gives off a single, posteriorly directed tubule and the same seems to be true of infraorbital 5 in 36472. In the remaining infraorbitals, both more or less defective, the sensory canal cannot be traced.

In the dermosphenotic in 38531 (Pl. 12, fig. 3) an antero-dorsally directed branch of the infraorbital sensory canal is clearly visible, giving off at least two short, dorsally directed tubules.

As in *Ph. crenulata*, nothing can be said concerning the various parts of the sensory canal in the dermopterotic and the origin of the preopercular sensory canal. In 36472 and 38531 the course of the sensory canal in the dermopterotic seems to be about the same as in *Ph. crenulata*.

Cephalic division of main lateral line

The cephalic division of the main lateral line passes over from the dermopterotic into the extrascapular. In 38531 (Pl. 12, fig. 3; Text-fig. 12) its course in this bone can be followed, in part at least, from near its antero-lateral corner to near its posterior end, mesially giving off the supratemporal commissure (s. com, Text-fig. 12) and laterally three postero-laterally directed tubules. The preserved lateral part of the supratemporal commissure gives off three tubules posteriorly.

The *preopercular sensory canal* (Text-fig. 12) has the same course along the middle of the preoperculum as in *Ph. crenulata*. Regarding the tubules given off from the posterior side of the canal, thirteen are clearly visible in 38531, but as the preoperculum is a little damaged at about its mid-point, there may be at least one more tubule. In P.1047 I have counted 14 tubules, but their arrangement is remarkably irregular ; in 36472 at least 12 tubules are visible, but one or two more tubules may be present in the anteriormost hidden part of the preoperculum. The total number of preopercular tubules in *Ph. limbata* may consequently be estimated as about 14 against about 17 in *Ph. crenulata*.

In P.1047 and 36472 the lateral surface of the preoperculum clearly shows the two grooves representing the posterior portion of the anterior division of the supramaxillary (horizontal) pit-line and the postmaxillary (vertical) pit-line respectively $(hc_1, orp, \text{Pl. II}, \text{figs. I}, 2; \text{Text-fig. I2})$. As in *Pholidophorus latiusculus* an anterior portion of the anterior division of the supramaxillary line is clearly visible on the lateral surface of infraorbital 3.

Regarding the mandibular sensory canal, nothing can be made out.

In 36472 the lateral surface of the angular possesses a small vertical groove, obviously the oral pit-line $(orp_1, \text{ Pl. 11, fig. 2})$.

Exoskeletal shoulder-girdle and squamation

The *suprascapula* and *supracleithrum* are preserved only in 38531, and then only as fragments which give very little information about their shape.

The *cleithrum* (*Cl*, Pl. 11, fig. 2; Pl. 12, fig. 3) is, to a certain extent, visible in 36472 and 38531; it seems to be proportionately smaller than that of *Leptolepis*. A deep, scale-like bony plate posterior to the suboperculum and cleithrum may be interpreted as a *postcleithrum* (*Pcl*, Pl. 12, fig. 3).

The scales are arranged in about 40 to 42 transverse rows counted from the hind margin of the operculum to the middle of the caudal fin ; posterior to the last row there are about 9 rows on the body axis dorsal to the lateral line, thus in all about 50 rows. On the body there are generally five longitudinal rows of enlarged scales, the deepest more than twice as deep as broad (proportionately deeper than in *Ph. crenulata*) and with the posterior margin finely serrated ; the number of small points on the posterior margin is approximately 15 on the largest scales or about as in pl. 37, fig. 4 of Agassiz (1843). All the scales, including the anterior ones, are comparatively thick, and I cannot see any concentric striations such as are present in *Ph. crenulata*.

Lateral line

Because of the defective state of the suprascapula and supracleithrum nothing can be made out regarding the lateral line in these bones. The anterior lateral line scales are also indistinct, but a few transverse rows behind the operculum the lateral line becomes very distinct and runs almost straight to the base of the middle caudal rays.

Paired and unpaired fins

The *pectoral fin* is similar to that of *Ph. crenulata*, the highest number of lepidotrichia seems to be 23, perhaps 24, thus a little lower than in the type species; it must, however, be kept in mind that the number of the small ventral lepidotrichia is difficult to determine.

The ventral fin has 12 clearly visible lepidotrichia in 38531, but as in *Ph. crenulata* there may have been about three more small ones; in P.3596 I have counted 14 lepidotrichia, the two innermost very small.

The *dorsal fin* has the same general shape as in *Ph. crenulata*. Also regarding the number of lepidotrichia there is no important difference. In 38531 there seem to have been about 14 lepidotrichia, the anterior ones preserved as impressions only; in the other specimens investigated the dorsal fin is more or less defective.

The anal fin also is similar to that in *Ph. crenulata*; the anterior part of this fin with its two anterior short lepidotrichia followed by the third long and fulcrated lepidotrichium is figured by Woodward (1919, pl. 22, fig. 6). The total number of lepidotrichia is about 13, perhaps up to 15 in P.1047*a*. In P.4422 the anal radials, 12 in number, are clearly exposed.

The caudal fin is hemiheterocercal as in Ph. crenulata.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.

Genus PHOLIDOPHOROPSIS nov.

PRELIMINARY DIAGNOSIS. Pholidophoridae of medium size, as far as known similar to *Pholidophoroides* but differing in the following features. Exoskeletal cranial bones without or with only very feeble ganoin ornamentation. Scales thin and cycloid with fine concentric striations.

TYPE SPECIES. Pholidophoropsis caudalis (Woodward).

Pholidophoropsis caudalis (Woodward)

(Pl. 13, Text-fig. 13)

1844 ? Leptolepis caudalis Agassiz, 2, 2: 133 (nom. nud.).

1895 Pholidophorus caudalis Woodward : 457, pl. 18, figs. 1, 2 (partim).

1941 Pholidophorus (? Pholidophoroides) caudalis Woodward ; Woodward : 90.

DIAGNOSIS. *Pholidophoropsis* of medium size, at least up to 120 mm. in total length. Greatest depth of body slightly more than one quarter of standard length (ca. 26-27% of that length). Depth of caudal peduncle slightly more than one-tenth (ca. 11%) of standard length. Maxillary proportionately not as deep as in *Ph. crenulata*. Preopercular sensory canal with about 10 tubules. Scales very thin.

HOLOTYPE. British Museum (Natural History) No. P.3664.

MATERIAL. Besides the holotype, specimens P.3664*a* (paratype) and 39871 belong to this species and have been used in the following description.

DESCRIPTION. The total length of the holotype is 120 mm.; P.3664*a* and 39871 have a total length of 95 mm. and 117 mm. respectively, but in both these specimens the tips of the caudal fin are broken, and the maximum length of the last named specimen may consequently have been at least 120 mm.¹ The standard length or length from the tip of the snout to the base of the middle caudal fin rays is about 100 mm. in the holotype, in the two other specimens 81 and 102 mm. respectively, but P.3664*a* seems to be a little shortened by pressure. The greatest depth of the body is slightly more than one quarter (26-27%) of the standard length and the depth of the caudal peduncle is about 11% of the standard length. The length of the head seems to be exactly one quarter of the standard length in the two larger specimens; in P.3664*a* this length is slightly greater because of the shortened standard length.

The ventral fins are situated about midway between the tip of the snout and the base of the caudal fin rays, and the distance between the base of the ventrals and the origin of the anal is about 70% of the distance between the bases of the pectoral and ventral fins. As in the species of the genus *Pholidophoroides* the dorsal fin is situated above the interspace between the ventral and anal fins; in P.3664*a* a forward displacement of the dorsal fin seems, however, to have occurred through pressure.

Good figures of the entire holotype and of P.3664*a* are given by Woodward (1895, pl. 18, figs. 1, 2).

^I Woodward (1895: 457) gives the length of *Ph. caudalis* as "about 0'13"; This obviously refers to 43055, described below (p. 416) as *Pholidophoropsis maculata* sp. nov.

All three specimens are more or less defective and the following description is consequently rather incomplete but sufficient for identifying the species and demonstrating its close affinity with members of the genus *Pholidophoroides* described above. As a general characteristic of *Ph. caudalis* it may be mentioned that the exoskeletal bones of the skull, as well as the scales, are rather thin and almost totally lack ganoin ornamentation.

Exoskeletal skull roof

A *premaxillary* (Pmx, Pl. 13, fig. 1; Text-fig. 13) is preserved in P.3664*a*; its denticulated ventral margin is visible, but as the other parts of the bone are hidden below the antorbital, its general shape cannot be stated.

The *rostral* cannot be identified with certainty in any of the specimens available. The *nasal* (*Na*, Pl. 13, figs. 1, 2; Text-fig. 13) is partly visible in P.3664*a*, but this bone too is to a great extent hidden below the antorbital; a bone fragment anterior to the frontal in the holotype may represent the posterior part of the nasal. From these two fragments it may be concluded that the nasal of this species does not differ very much from the corresponding bone in *Ph. crenulata*.

The *frontal* (Fr, Pl. 13, figs. 1, 2; Text-fig. 13) seems to be rather broad in its anterior part and its dorsal surface bulges along the anterior part of the supraorbital sensory canal. The posterior, broad part of the frontal is defective and nothing of its posterior margin can be made out. The suture between the frontals of both sides is straight anteriorly but then makes an S-shaped bend to the left and to the right, clearly visible on the holotype.

The anterior part of a rather strong *supraorbital* (So, Pl. 13, fig. 2; Text-fig. 13) obviously similar to that in *Ph. crenulata*, is present in the holotype.

The dermosphenotic and the parietal are not discernible.

In the holotype parts of the *dermopterotic* and *extrascapular* (*Dpt*, *Ext*, Pl. 13, fig. 2; Text-fig. 13) are exposed but are insufficient to allow any detailed description.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pl. 13, figs. 1, 2; Text-fig. 13) is best preserved in P.3664a; it has, on the whole, the same shape as in *Ph. crenulata* with the characteristic convexity on the dorsal margin, but the longitudinal striation on the lateral surface is not nearly so pronounced. The posterior margin is partly crushed, but may have been notched in the same way as *Ph. crenulata*. The main difference from that species, apart from the lesser depth of the bone, lies in the presence of a delicate dentition along the whole ventral margin, not confined to its posterior half only.

The two supramaxillaries $(Smx_1, Smx_2, Pl. 13, fig. 1; Text-fig. 13)$ have the same general shape as in *Ph. crenulata*, but judging from P.3664*a* in which they are best preserved and well exposed, the antero-dorsal corner of supramaxillary 2 seems to be more markedly drawn out into a short process. Both supramaxillaries show a faint concentric striation on their lateral surface.

The bones of the infraorbital series are, for the most part, badly preserved.



FIG. 13. Pholidophoropsis caudalis (Woodward). Attempted restoration of head in lateral view. $\times 5$.

Ang, angular; Ant, antorbital; De. Spl, dentary; Dpt, dermopterotic; Ext, extrascapular; Fr, frontal; Ifo_1, Ifo_3-Ifo_5 , infraorbitals 1 and 3 to 5; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pa, parietal; Pmx, premaxillary; Pop, preoperculum; Ro, rostral; Smx_1 , Smx_2 , anterior and posterior supramaxillaries; So, supraorbital; Sop, suboperculum; *ifc. com*, ethmoidal commissure; *poc*, preopercular sensory canal; *s. com*, supratemporal commissure; *soc*, supraorbital sensory canal.

The antorbital (Ant, Pl. 13, figs. 1, 2; Text-fig. 13) is present in P.3664 and P.3664a, but in both the postero-dorsal part is broken off. Judging from the last named specimen it seems, however, that the antorbital in this species is shorter than in *Ph. crenulata*.

Infraorbital I (lachrymal) (If o_1 , Pl. 13, fig. 2; Text-fig. 13) can be traced in the holotype only, but the fragment gives no information as to the shape of the bone.

Infraorbital 2 is missing in all the three specimens available.

An *infraorbital* 3 (*Ifo*₃, Pl. 13, fig. 2; Text-fig. 13) is present in the holotype as well as in 39871. It has the ordinary shape with the antero-ventral margin slightly concave and the posterior margin rounded.

Of the remaining bones in the infraorbital series, a small *infraorbital* 4 is present in the holotype (Ifo_4 , Pl. 13, fig. 2). Two fragments in P.3664*a* may represent infraorbitals 4 and 5.

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A suborbital bone (Sbo, Pl. 13, fig. 2) is visible in the holotype, but its posterior margin is not distinguishable. Dorsal to this bone there is a small tongue-like bone similar to the small bone or bones dorsal to the suborbital in *Ph. crenulata* (see p. 398).

The *preoperculum* (*Pop*, Pl. 13, figs. 1, 2; Text-fig. 13) is more or less defective in the specimens available; it is best preserved in the holotype and has the same general shape as in *Ph. crenulata*, but its ventral, antero-ventrally directed limb diminishes markedly in depth towards the tip of the bone.

The operculum, the suboperculum and the interoperculum are partly preserved in the holotype and, as far as can be judged, they have the same general shape as the corresponding bones in *Ph. crenulata*.

Lower jaw

The lower jaw is visible to a great extent in P.3664*a* (*De. Spl, Ang, Pl. 13, fig. 1*), but as in most specimens of the two *Pholidophoroides* species described above, its dorsal margin is covered by the maxillary and therefore neither the entire outline of the lower jaw nor its depth can be determined. The lateral surface of the dentary has a longitudinal crest, obviously corresponding to the well-marked ridge between the dental and splenial parts of the dentary in *Ph. crenulata*, but ventral to this crest there are no traces of the rich ganoin ornamentation characteristic of this species and of *Ph. limbata*.

Sensory canal system of head

The supraorbital sensory canal (soc, Pl. 13, fig. 2; Text-fig. 13) in the nasal is partly visible in P.3664*a* as a short, laterally curving canal, representing the anteriormost part of this sensory canal. In the holotype no canal can be seen with certainty in the preserved posterior fragment of the nasal.

The frontal part of the supraorbital sensory canal has the same general course as in *Ph. crenulata* and is best exposed in the left frontal of the holotype. Its anterior, straight part is marked by a bulging of the dorsal surface of the bone, and on this part there is a small dorsal pore. At the postero-lateral curve the canal gives off from its mesial side a posteriorly directed tubule and from the lateral side at least two short, laterally directed tubules; more posteriorly the sensory canal cannot be followed. The main difference from the supraorbital sensory canal in *Ph. crenulata* is that the tubules are given off mainly from the lateral side of the canal in *Ph. caudalis* but from the mesial side in *Ph. crenulata*.

The *infraorbital sensory canal* is clearly visible in the antorbital bone of the holotype as well as in P.3664*a*; it gives off a posteriorly directed antorbital branch. For the rest the infraorbital sensory canal can only be traced as a slightly bent canal in infraorbital 3, giving off three postero-ventrally directed tubules in the holotype and in 39871. In the holotype infraorbital 4 shows a single tubule given off from the posterior side of the canal, for the rest the infraorbital sensory canal cannot be followed.

Cephalic division of main lateral line

In the holotype the sensory canal in the dermopterotic can be traced parallel to the dorso-lateral margin of the bone, but only a single pore on its dorsal surface can be observed. In the extrascapular the main canal and the supratemporal commissure are rather clearly visible (Pl. 13, fig. 1; Text-fig. 13). No tubules from the main canal are, however, discernible, but the supratemporal commissure gives off from its posterior side at least four backwardly directed tubules, decreasing in length towards the mid-line of the skull.

The *preopercular sensory canal* pierces the preoperculum in the middle of its length, as in *Ph. crenulata*. The tubules given off from its morphologically posterior side are short and straight; their number cannot be determined exactly, but they are obviously less numerous than in *Ph. crenulata*; in the dorsal limb of the bone only one tubule is visible dorsal to the posterior, ill-defined angle between the dorsal and ventral limbs, but as the upper part of the dorsal limb is not well exposed, there may be one or more tubules in the dorsal limb of the preoperculum. In the ventral limb, well exposed in the holotype, eight tubules are visible.

The mandibular sensory canal cannot be seen.

Exoskeletal shoulder girdle and squamation

Because of the bad state of the material available very little can be determined of the bones belonging to the exoskeletal shoulder girdle; nothing seems, however, to indicate that they are of special interest as species characteristics.

The squamation consists of very thin scales forming, where they are preserved, a continuous thin layer, generally without marked boundaries between the individual scales. In the holotype some scales are, however, clearly visible; they are thin with a delicate concentric striation, and their posterior margins are rounded and not serrated. It must, however, be noted that in P.3664*a* and 3987r some of the posteriormost scales are markedly thicker than the body scales.

A lateral line cannot be traced in any of the three specimens investigated.

Axial skeleton and paired and unpaired fins

The axial skeleton consists, as in *Ph. crenulata*, of rather thin ring-vertebrae. The shape and number of the abdominal vertebrae is difficult to state; the centra of the caudal vertebrae are, judging from P.3664*a*, about twice as deep as broad.

The best preserved *pectoral fin*, that of P.3664*a*, shows 21 lepidotrichia, but it is not quite certain that the series is complete. The first, strong lepidotrichium is fulcrated.

The *ventral fin* has, in the same specimen, 15 clearly visible lepidotrichia; the first ones are, however, defective, and no fulcra could be seen.

The dorsal fin is similar to the corresponding fin in *Ph. crenulata*, including the presence of fulcra; in 39871 I have counted 15 lepidotrichia. The radials, clearly visible in this species because of the thin scale covering, in the holotype number at least 14, in P.3664a about 14 and in 39871 thirteen.

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The *anal fin* is likewise similar to that of *Ph. crenulata*, but the number of lepidotrichia cannot be determined. The number of radials is eleven in both the holotype and P.3664*a*; in 39871 there must have been more than the 9 radials still preserved.

The *caudal fin* is hemi-heterocercal as in *Ph. crenulata* and *Ph. limbata*, and with the dorsal and ventral margins densely set with small fulcra.

REMARKS. The two best preserved specimens of this species, the holotype and P.3664*a*, could be studied only during short visits to London and therefore it is quite possible that a closer investigation of them will reveal details not mentioned in the description given above. It is my hope, however, that this description will be sufficient for the identification of the species as well as providing a suitable basis for a discussion regarding its affinities and taxonomic position.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.

Pholidophoropsis maculata sp. nov.

(Pl. 14, Text-figs. 14, 15)

1895 Pholidophorus caudalis Woodward : 457 (partim).
1895 Pholidophorus limbatus Agassiz ; Woodward : 466 (partim : P.7582).

DIAGNOSIS. *Pholidophoropsis* of medium size, at least up to about 160 mm. in total length. Greatest depth of body about one quarter of standard length. Maxillary comparatively slender. Preopercular sensory canal with about 14 tubules. External bones of skull with scattered ganoin spots and streaks. Scales comparatively large, thin, with concentric striae and with posterior margin rounded ; axillary scales with ganoin spots.

HOLOTYPE. British Museum (Natural History) No. 43055.

MATERIAL. Besides the holotype, P.7582, listed by Woodward under *Pholidophorus limbatus* as "Imperfect skeleton probably of this species", shows such striking similarities with the holotype that both undoubtedly belong to one and the same species. It has also been used for the following description, but its defective state of preservation allows only some complementary additions to the description of the holotype.

DESCRIPTION. The total length of the holotype is about 127 mm. (Pl. 14, fig. 1). Woodward's (1895:457) statement that the maximum length of his *Ph. caudalis* is "about 0.13" is obviously founded on this specimen. The length from the tip of the snout to the hind margins of the hypurals (standard length) is about 109 mm. The total length of P.7582 cannot be measured; the skull together with the vertebral column to the posterior margin of the hypurals (standard length) is about 133 mm. and the total length may be estimated as about 160 mm. The greatest depth of the body in the holotype is 27 mm. or almost exactly one quarter of the standard length; the caudal peduncle is crushed dorso-ventrally and its depth cannot therefore be measured. The length of the head in the holotype cannot be stated with accuracy

(the opercular bones seem to have been displaced backwards through pressure) but it may be a little greater than the maximum depth of the body. In P.7582 the length of the head is about one quarter of the standard length.

The position of the dorsal, ventral and anal fins is somewhat different from that in the species described above. The base of the ventral fin is situated a little nearer to the tip of the snout than to the hind margins of the hypurals, and the distance between the base of the ventrals and the origin of the anal is about 85% of the distance between the bases of the pectorals and the ventrals. The dorsal fin is situated somewhat further back, beginning about midway between the base of the ventrals and the anal origin and ending above the last named fin.

The skull is more or less defective in both specimens investigated ; consequently the following description must be considered as provisional.

Exoskeletal skull roof

A *premaxillary* is not preserved in either of the specimens available.

In the holotype the *rostral* seems to be well developed, but its shape cannot be determined in any detail.

The *nasal* (Na, Pl. 14, fig. 2; Text-figs. 14, 15), preserved only in the holotype, is a broad, almost leaf-like bone with the antero-lateral margin concave, obviously constituting the postero-mesial limit of the anterior nasal opening. The dorsal surface of the nasal is ornamented with ganoin spots.

The *frontal* (Fr, Pl. 14, fig. 2; Text-figs. 14, 15) has a typical shape, with the broadest part posterior; its anterior, narrower part is hidden below the nasals in the holotype and defective in P.7582, but seems to be short, perhaps comparatively shorter than in *Ph. crenulata*. In the holotype the suture between the frontals of both sides is straight anteriorly and then makes an S-shaped bend to the right and to the left.

The supraorbital (So, Pl. 14, fig. 2; Text-figs. 14, 15) is only partly preserved in the holotype, but seems to have approximately the same general shape as in Ph. crenulata. In P.7582 the supraorbital is lacking.

A dermosphenotic is not visible in either of the specimens investigated.

The shape of the *parietal* (Pa, Pl. 14, fig. 2; Text-figs. 14, 15) cannot be determined, but as the dermopterotic is comparatively broad in the mesio-lateral direction, the exposed dorsal surface of the parietal may be smaller than in *Ph. crenulata*.

The *dermopterotic* (*Dpt*, Pl. 14, fig. 2; Text-figs. 14, 15) is clearly visible on the right side in the holotype and on the left side in P.7582, showing that its mesio-lateral breadth is comparatively large. The surface of the dermopterotic, like that of the frontal and the parietal, has an ornamentation of small, partly confluent ganoin spots.

The lateral part of a bone, possibly the *extrascapular*, is visible posterior to the dermopterotic in both specimens, but this interpretation is rather uncertain as no traces of a sensory canal or of tubules can be seen.

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FIG. 14. Pholidophoropsis maculata sp. nov. Attempted restoration of head in lateral view. $\times 4^{\circ}2$.

Ant, antorbital; De. Spl, dentary; Dpt, dermopterotic; Fr, frontal; Ifo₁, Ifo₃-Ifo₅, infraorbitals I and 3-5; Iop, interoperculum; Mx, maxillary; Na, nasal; Op, operculum; Pa, parietal; Pop, preoperculum; Ro, rostral; Sbo, suborbital; Sop, suboperculum; ant. br, antorbital branch of infraorbital sensory canal; hc_1 , anterior division of supramaxillary pit-line; ifc, infraorbital sensory canal; ifc. com, ethmoidal commissure; orp, post-maxillary pit-line; poc, preopercular sensory canal.

Dermal bones of cheek and opercular apparatus

The maxillary (Mx, Pl. 14, fig. 2; Text-fig. 14) is, in its anterior, mesially directed part rather delicate; its lateral, posteriorly directed part increases in height backwards. Its height cannot be measured exactly, but it seems to be about the same as in *Ph. caudalis*. The convexity of the anterior part of the dorsal margin of the maxillary exists, but it is not as pronounced as in *Pholidophoroides* species. The ventral margin of the maxillary is not exposed in the holotype and only for a short distance anteriorly in P.7582, but here traces of a delicate dentition are visible, indicating that probably the whole ventral margin is denticulate as in *Ph. caudalis*. The lateral surface of the posteriorly directed part of the maxillary is richly ornamented; in the holotype a few longitudinal striations parallel to the dorsal margin recall the striation in *Ph. crenulata*, but below them there are numerous short ganoin streaks and spots.

Only supramaxillary 1 of the *supramaxillaries* is preserved in the holotype, and it is defective $(Smx_1, Pl. 14, fig. 2)$; in P.7582 both supramaxillaries are exposed.

Supramaxillary I seems to be relatively broader than in *Ph. crenulata*, its anterior tip being longer, and the striation on its lateral surface not as well marked as in that species, particularly not in P.7582, where only a few ganoin streaks are visible. Supramaxillary 2 (Smx_2 , Text-fig. 14), preserved in a defective state, has about the same shape as in *Ph. caudalis*, but its lateral surface practically lacks ornamentation. As in the *Pholidophoroides* species, the supramaxillaries do not overlap the dorsal margin of the maxillary.



FIG. 15. Pholidophoropsis maculata sp. nov. Attempted restoration of head in dorsal view, the snout flattened. \times 4'2. Lettering as in Fig. 14.

The bones of the infraorbital series are only partly preserved.

The antorbital (Ant, Pl. 14, fig. 2; Text-figs. 14, 15), only visible in the holotype, seems to have a broad triangular shape, not as elongate as in *Ph. crenulata*.

In both specimens *infraorbital* 1 (*lachrymal*) (*Ifo*₁, Pl. 14, fig. 2) is only preserved as fragments without traces of the sensory canal or of its tubules.

Infraorbital 2 is lacking.

Infraorbital 3 (Ifo₃, Pl. 14, fig. 2; Text-fig. 14) is, judging from the exposed part, almost semicircular in the holotype; in P.7582 its dorsal margin is defective, but also in this specimen infraorbital 3 is by no means as broad as in the *Pholidophoroides* species.

Dorsal to infraorbital 3 in the holotype there are two small bones which obviously represent *infraorbitals* 4 and 5 (Ifo_4 , Ifo_5 , Pl. 14, fig. 2; Text-fig. 14).

Posterior to infraorbitals 3–5 there are, in the holotype, some bony plates which may be fragments of a *suborbital* bone; the lateral surface of these fragments is ornamented with ganoin spots. In P.7582 there are some bone fragments ventral to the dermopterotic; they have also been interpreted as parts of a suborbital.

The *preoperculum* (*Pop*, Pl. 14, fig. 2; Text-fig. 14), best preserved in the holotype, is only slightly arched; it is of almost the same height in the middle and in the ventral parts of the bone; the dorsal limb seems to taper dorsally, but here the outline of the bone is difficult to follow. The middle and dorsal parts of the preoperculum have a surface ornamentation of lustrous ganoin spots; such spots are lacking on the dorsal part of the ventral limb, probably indicating that this part of the bone is normally covered by the posterior end of the maxillary. In P.7582 the preoperculum is only partly preserved.

In the holotype the operculum (Op, Pl. 14, fig. 2) seems, at first sight, to be very low compared with the corresponding bone in *Ph. crenulata*, but its postero-ventral part is pressed in below the suboperculum and therefore its outline cannot be determined accurately. In P.7582 the operculum is partly crushed, but its ventral part is well exposed, showing that this bone has the same general shape as in the *Pholidophoroides* species. The lateral surface of the operculum is ornamented with ganoin spots.

The suboperculum (Sop, Pl. 14, fig. 2; Text-fig. 14), preserved only as fragments in both specimens, has the same general shape as in the *Pholidophoroides* species; its antero-dorsal process is well developed. Like the operculum its lateral surface is ornamented with ganoin spots.

Only small fragments of the *interoperculum* (*Iop*, Text-fig. 14) are exposed in the holotype, in P.7582 its posterior part is exposed; the lateral surface of this part shows a few ganoin spots.

Lower jaw

Only parts of the *dentary* (*De. Spl,* Pl. 14, fig. 2; Text-fig. 14) are exposed and they give little information regarding its shape. Anteriorly the dental part is, however, only gently ascending, its lateral surface is smooth and no teeth can be seen along its margin. The splenial part is separated from the dental by a well-marked ridge, ornamented with ganoin, and its lateral surface is, at least partly, provided with small ganoin spots and short streaks.

Sensory canal system of head

The sensory canal system of the head can be traced only in part.

The supraorbital sensory canal pierces the nasal as an arched canal from its anterolateral corner to its posterior end. On the left nasal an elevated pore is visible near the anterior end of the canal, other pores or tubules cannot be seen. In the frontal the canal can only be traced imperfectly, but it seems to have the same course as in *Ph. crenulata*; only a few short tubules from the mesial side of the canal are visible. The canal probably ends in the parietal, but its presence there cannot be established. In the rostral there is an ethmoidal commissure (*ifc. com*, Pl. 14, fig. 2; Text-figs. 14, 15) joining the infraorbital sensory canals of both sides. This canal begins in the antorbital, in which it gives off posteriorly an antorbital branch. As the fragmentary infraorbital I (lachrymal) has no remains of the sensory canal and as infraorbital 2 is missing, nothing can be said regarding the part of the canal belonging to these bones. In infraorbital 3 of the holotype the canal is weakly arched and posteroventrally gives off four diverging tubules with small ganoin spots on their surface; the anterior tubule is about half the length of the others. In specimen P.7582 the canal and its tubules are indistinct. In each of the infraorbitals 4 and 5 the canal gives off a single, posteriorly directed tubule. The further course of the infraorbital sensory canal is unknown.

Cephalic division of main lateral line

A deep arched groove on the parietal in the holotype may represent the middle pit-line $(m\phi, Pl. 14, fig. 2)$.

On the lateral margin of the dermopterotic a single pore is visible in both specimens, indicating that the infraorbital sensory canal and the cephalic division of the main lateral line pierce this bone near its lateral margin. The further course of the main lateral line is not visible.

The *preopercular sensory canal* pierces the preoperculum in the middle of its length as in the *Pholidophoroides* species. From its morphologically posterior side it gives off 13 or 14 tubules in the holotype; the three anterior tubules are short and straight and are followed by four longer, straight tubules; posterior to the latter there are two long and slender tubules and posterior to them there can be traced four wider tubules, separated by wider interspaces; three of these tubules are situated dorsal to the posterior angle of the preoperculum. It cannot be stated with accuracy whether one more tubule exists in the dorsalmost part of the preoperculum. In the defective preoperculum of P.7582 only a few tubules are visible.

Little can be said about the *mandibular sensory canal* except that there is a series of short, backwardly directed tubules on the lateral surface of the splenial part of the dentary.

Exoskeletal shoulder girdle and squamation

The suprascapula and the supracleithrum cannot be identified. A rather strong cleithrum (Cl, Pl. 14, fig. 2) is partly exposed in P.7582 and the dorsal part of the same bone is visible in the holotype. Posterior to the dorsal part of the cleithrum parts of a rather large *postcleithrum* (Pcl, Pl. 14, fig. 2) with ganoin spots on its lateral surface are visible in both specimens.

The squamation is well preserved in the holotype. The scales are large and remarkably thin with a delicate concentric striation; their posterior margin is rounded and not serrated. The middle flank scales seem to be somewhat larger than the others. The axillary scales dorsal to the pectoral fin, also present in P.7582, are ornamented with ganoin spots. No lateral line scales can be distinguished.

Axial skeleton and paired and unpaired fins

The *axial skeleton* is entirely exposed in P.7582, but the separate ring-vertebrae are partly crushed and partly embedded in the rock and cannot be studied in any detail; their number cannot be stated with accuracy, but it seems to be about 48.

The *pectoral fin* is not entirely exposed in either of the two specimens available and consequently the number of lepidotrichia cannot be given. The first, strong lepidotrichium is fulcrated (Fu, Pl. 14, fig. 2).

The ventral fin can only partly be seen in the holotype, but in P.7582 both ventral fins are well exposed and in the right one 14 lepidotrichia can be counted, the two first ones comparatively short; the third is densely set with fulcra, also visible in the holotype. As already mentioned by Woodward (1895 : 466) the right basipterygium is preserved in P. 7582; the basipterygium can also be traced in the holotype.

All lepidotrichia in the *dorsal fin* are missing from the holotype, but parts of its anterior radials and some impressions indicate the position of the fin. In P.7582 the dorsal fin is rather well preserved with at least 13 lepidotrichia visible, the second one with a series of fulcra along its anterior margin; anterior to the first clearly visible lepidotrichium there are traces of one or two short lepidotrichia. The first radial is V-shaped and composed of two fused radials.

Of the *anal fin*, 9 clearly visible radials are preserved in the holotype. In P.7582 TO lepidotrichia and 5 radials can be seen, but as the anterior lepidotrichia are only exposed basally, it is impossible to say whether fulcra are present or not.

The *caudal fin* may be hemi-heterocercal as in the *Pholidophoroides* species, but as the fulcra on the dorsal margin are pressed down over the upper part of the caudal peduncle in the holotype and as the caudal fin is practically wanting in P.7582, nothing can be said regarding the true shape of this fin.

REMARKS. It is only with some hesitation that I have created a new species for the specimens 43055 and P.7582. In many respects they are very similar to Ph. *caudalis* (to which species Woodward referred specimen 43055), particularly in having thin scales of the same shape as in the holotype of Ph. *caudalis*. There are, however, many differences. In Ph. maculata the dorsal fin seems to be situated more posteriorly than in Ph. *caudalis*, the exoskeletal cranial bones are thicker in Ph. maculata than in Ph. caudalis and, moreover, richly ornamented with ganoin spots, infraorbital 3 and the preoperculum are differently shaped, and the number and position of the tubules belonging to the preopercular sensory canal are also different in the two species. All these facts seem to me to preclude the identification of 43055 and P.7582 as Ph. caudalis. It must, however, be remembered that our present knowledge regarding these species is rather defective, and a definitive solution to this question needs more and better preserved material. At present I find it most convenient to keep the two types apart as separate species.

HORIZON AND LOCALITY. Lower Lias; Lyme Regis, Dorset.
III. DISCUSSION

(a) The taxonomic relationship between the genera and species within the family Pholidophoridae s. str. and a preliminary diagnosis of the family

The description of the exoskeletal cranial bones in Pholidophorus bechei given above differs in some respects from that given by Miss Rayner (1948). The greatest difference concerns the shape of the antorbital and the course of the supraorbital and infraorbital sensory canals in the snout. The conditions described by Miss Rayner, already doubted by Griffith & Patterson (1963: 32), can hardly be correct. Although I had no specimen with the exoskeletal bones of the snout preserved in their natural mutual position I think that my attempted reconstruction (Text-figs. 1, 2) comes nearer to the true conditions. This interpretation seems also to be corroborated by the arrangement of the corresponding structures in the well-preserved Pholidophoroides crenulata. Moreover, the material at my disposal clearly shows that the nasals do not meet in the median line but are separated by the anterior parts of the frontals. Apart from minor corrections regarding the shape of some bones such as the premaxillary, supraorbital I, the dermosphenotic and the preoperculum, it has been possible to add some more details regarding the tubules of the sensory canal system.

Our present knowledge of *Pholidophorus bechei*, the type species of the genus *Pholidophorus*, is of course far from complete but it seems sufficient to serve as the basis for a discussion of taxonomic affinities, *i.e.* which other species may be referred to the genus *Pholidophorus* in a restricted sense and which species may be considered as belonging to other genera.

A species which, as far as could be made out, agrees with *Ph. bechei* in all features of generic value is *Ph. latiusculus* from the Upper Trias of Seefeld, Tyrol. Unfortunately the shape of the rostral and antorbital bones with their sensory canals are still unknown, but in other respects the agreement between the two species is so close that they must be considered congeneric. Consequently the diagnosis of the genus *Pholidophorus* s. str. given on p. 356 is based on these two species.

The species *Ph. caffii* from the Upper Trias of Viciarola, North Italy, considered by most authors as a synonym of *Ph. latiusculus*, is beyond doubt a distinct species. In many respects strikingly similar to *Ph. bechei* and *Ph. latiusculus*, it differs from both in some important respects, above all in the shape of the preoperculum and the preopercular sensory canal. The presence of only a single supramaxillary, if not merely an individual anomaly, is moreover a feature separating it from the two *Pholidophorus* species mentioned. Its reference to the same genus as those two species would widen the conception of the genus *Pholidophorus* rather excessively. On the other hand I find it at present inadvisable to create a new genus for a species founded on a single, defective specimen, in most respects similar to the true members of that genus, and therefore I have provisionally attributed it to *Pholidophorus*.

The specimen described above as Ph. cf. *pusillus* represents a species which, as far as can be judged from the partly incomplete material, seems to agree with Ph. *bechei* and Ph. *latiusculus* in all characters of generic value. Consequently it may be placed,

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at least provisionally, in the genus *Pholidophorus* s. str. Whether it really belongs to *Ph. pusillus* Agassiz is a question which at present must be left unanswered.

The rather numerous but unfortunately badly preserved specimens from the Lower Lias of Lyme Regis. Dorset, which I have described above under the species name dorsetensis, were referred to Ph. caudalis by Woodward (1805). They have, however, nothing to do with the true Ph. caudalis but show, as far as known, many similarities with *Ph. bechei* and *Ph. latiusculus*. The preoperculum, one of the most characteristic bones of those preserved, shows the same notch on its posterior margin as in the two species mentioned and the arrangement of the tubules belonging to the preopercular sensory canal is about the same as in those species, but the canal itself runs still nearer to the anterior margin of the bone, about as in Leptolepis. Further, the extension of the two supramaxillaries over almost the whole dorsal margin of the maxillary recalls a condition similar to that in Leptolepis, and the squamation consists of comparatively thin cycloid scales. The lower jaw is, however, only gently ascending anteriorly, not abruptly as in Leptolepis, and the nasals are comparatively large. In many respects these specimens are thus similar to the members of the genus Pholidophorus s. str., in others to Leptolepis, but they can, in my opinion, be placed neither in Pholidophorus nor in Leptolepis. Consequently I have proposed for the species dorsetensis a new genus, Pholidolepis, the preliminary diagnosis of which is given above (p. 387).

The genus *Pholidophoroides* was created by Woodward for the species *Pholidophorus* crenulatus and founded mainly on some scale characteristics and on the stoutness of the maxillary (see p. 393). Re-examination of the type species of the genus has revealed many other characteristics, especially a high number of infraorbitals (more than five), a rather broad preoperculum with the preopercular sensory canal running along the middle of the bone and with rather short and straight tubules in its ventral limb, and the presence of only a single supraorbital bone. Consequently, it seems to me that Woodward was quite correct in creating the genus *Pholidophoroides*. A further species showing, in general, the same characteristics is *Pholidophorus limbatus*, which therefore must be considered a second species of the genus.

Woodward thought that his *Ph. caudalis* probably belonged to his new genus *Pholidophoroides*. As far as the partly defective material makes comparison possible, it is quite obvious that *caudalis* is, in many respects, very similar to other members of that genus; above all the preoperculum, the preopercular sensory canal and its tubules have the same characteristic shape in *caudalis* as in *Pholidophoroides*. There seems, moreover, to be only a single supraorbital. The exact number of infraorbitals is, unfortunately, indeterminable but nothing indicates that their number is more than five; if this be so there is, in this respect, a difference of taxonomic importance between *caudalis* and the two *Pholidophoroides* species. The most striking difference between them is, however, that the squamation in *caudalis* consists of rather thin cycloid scales, in *Pholidophoroides* of thick ganoin scales. This difference in squamation prevents, in my opinion, *caudalis* being placed in the genus *Pholidophoroides* and because of this I have created for it the new genus *Pholidophoropsis*.

As a second *Pholidophoropsis* species I have, albeit with some hesitation, described two imperfect specimens under the new trivial name *maculata*. The reasons for the creation of this species are discussed on p. 422. In this connexion it must, however, be remembered that differences in the ganoin covering of the exoskeletal cranial bones may be dependent on ontogenetic age, as described for *Ph. bechei*, and that the *maculata* specimens may merely represent older individuals of *caudalis*. But as the largest *caudalis* specimen is 120 mm. in length, the smallest *maculata* 127 mm., the difference in respect of the absence or presence of ganoin spots should not be as pronounced as it actually is if the ganoin spots are a feature characterizing only the largest specimens.

The genera and species considered here are more or less closely related and constitute a family Pholidophoridae in a restricted sense; a possible exception is the genus *Pholidolepis*, the systematic position of which cannot be determined until we have a better knowledge of the genus *Leptolepis*. This discussion must be deferred until a revision of that genus, now in preparation, is completed. It is of course very probable that many other species will be added to this family as soon as the members of the old genus *Pholidophorus* become better known.

Griffith & Patterson (1963) have in their valuable monograph on Ichthyokentema purbeckensis compared this genus with Pholidophorus as represented by Ph. bechei and Ph. similis Woodward. For this reason I must briefly mention the last named species although I have not yet had the opportunity of studying it myself. According to the description of Ph. similis given by de Saint-Seine (1949) there are so many dissimilarities between that species and the members of Pholidophorus s. str. described above, that it cannot be maintained in this genus. I need mention only the curious shape of the two postorbital infraorbitals (the dorsal one obviously corresponding both to infraorbitals 4 and 5 and to the dermosphenotic in Pholidophorus), the different shape of the maxillary, the suborbital, the preoperculum, the outline of the lower jaw and so on. All these features are atypical for the genus Pholidophorus as represented by Ph. bechei and Ph. latiusculus and most of them do not occur in the other pholidophorids described above. However, as I have no personal information regarding Ph. similis I shall confine myself to these comments.

Griffith & Patterson (1963) have convincingly shown that *Ichthyokentema purbeckensis* represents a family of its own, Ichthyokentemidae, and have given (p. 6) an exhaustive diagnosis of the new family. For the family Pholidophoridae as understood here no such diagnosis can be given at present because of our imperfect knowledge, particularly regarding the endocranium and many other details. The following diagnosis must therefore be considered a preliminary one.

Family PHOLIDOPHORIDAE s. str.

PRELIMINARY DIAGNOSIS. Fusiform Pholidophoriformes of small to medium size; bones of head and scales with or without ganoin covering; rostral toothless, not separating premaxillaries; nasals not in contact in the mid-line; dermosphenotic not elongated dorso-ventrally; five to seven infraorbitals, infraorbital 3 the largest; one to two supraorbitals; two supramaxillaries (except in *Ph.* (?) *caffui*?); mandible

gently ascending, with dentary (dentalo-splenial), articular and angular (angulosupra-angular); dentition on premaxillary, maxillary and dentary, only weakly developed on two last named bones; single gular; preoperculum more or less angular; suture between operculum and suboperculum oblique; supraorbital sensory canal ending in parietal and having no anastomosis with infraorbital sensory canal; anterior and middle pit-lines on parietal, middle pit-line extending on to dermopterotic; preopercular sensory canal with moderate to rather long tubuli; preoperculum with anterior division of supramaxillary (horizontal) and postmaxillary (vertical) pit-lines, former sometimes with anterior portion on infraorbital 3; oral pit-line present on angular; vertebrae, as far as known, with annular centra; fulcra present on all fins (except in *Pholidolepis*); scales more or less rhomboid with smooth or pectinated hind edge, or cycloid with fine concentric striation; some longitudinal rows of deepened scales on the flank.

(b) Some phylogenetic aspects of the genera and species within the family Pholidophoridae s. str.

The genera and species of the family Pholidophoridae treated above are, as previously stated, more or less closely related. Their phylogenetic relationship is of course difficult to discuss on the basis of our present knowledge, but some comments may be appropriate.

The pholidophorids are generally considered to be advanced holosteans, probably the forerunners of the teleostean stage of development within the actinopterygians. One of the most striking differences between the holostean and teleostean stages is the transformation of the thick, ganoin-covered scales into thin cycloid scales. This trend of evolution is clearly demonstrated in the species now under consideration. The Upper Triassic species Pholidophorus latiusculus, Ph. cf. pusillus and Ph. (?) caffii as well as the Lower Liassic Pholidophoroides limbata have thick scales, in Ph. crenulata the anterior body scales are thinner and show, as stated by Woodward (1941), a concentric striation, and in *Pholidophorus bechei* the younger individuals show a weaker ganoin covering of the exoskeletal cranial bones and scales than do the adult specimens. In Pholidophoropsis maculata the ganoin covering on the exoskeletal cranial bones is confined to small scattered spots and streaks, whilst of the thin cycloid body scales, only some axillary scales carry a few ganoin spots; thicker ganoin scales exist only at the caudal fin base. In Ph. caudalis no ganoin spots are visible on the exoskeletal cranial bones or axillary scales; thicker scales occur only at the posterior end of the caudal peduncle as in *Ph. maculata*. In Pholidolepis dorsetensis a ganoin ornamentation is present at least on the maxillary, the supramaxillaries and the lower jaw, whereas the body scales are thin with a delicate concentric striation. This may indicate that these pholidophorids are at that phylogenetic stage at which the reduction of the ganoin covering of the scales is taking place, and further, that this reduction began in the anterior part of the body and that the posterior part of the caudal peduncle retained the ganoin scales longer.

These consecutive stages of scale reduction indicate, however, certainly not a straight phylogenetic series, which is evident from other facts.

The shape of the preoperculum together with the course of the preopercular sensory canal and the pattern of its tubules seem to be very useful indicators of the relationship between various taxonomic units. In the family Pholidophoridae s. str. the most primitive type is represented by the broad and little curved preoperculum in Ph. (?) caffii; the preopercular sensory canal runs in the dorsal limb of the bone somewhat nearer to its posterior than to its anterior margin, in the ventral limb it runs in about the middle of its length. The tubules given off from the posterior side of the canal are comparatively few, wide and rather short. From this rather primitive preopercular type one can easily derive that of Ph. cf. pusillus; the general shape of the preoperculum is about the same, but the preopercular sensory canal runs nearer to the middle of the bone and the tubules are more numerous in the ventral part of the bone and are, moreover, longer. A further stage is represented by Ph. latiusculus. Here, the preoperculum is more differentiated in that its dorsal and ventral parts are of a different shape and its posterior margin possesses a shallow notch ; the preopercular sensory canal runs a little nearer to the anterior than to the posterior margin of the bone and its tubules are more numerous; in the ventral part of the bone the tubules are rather long and slightly curved. The preoperculum of *Ph. bechei* has a fairly characteristic shape ; its anterior margin is slightly concave, its posterior margin is notched and its postero-ventral corner projects backwards. The number of tubules belonging to the preopercular sensory canal is even greater than in Ph. latiusculus and those in the ventral limb of the bone are still longer. The preoperculum of *Pholidolepis dorsetensis* recalls many of the characteristics of *Ph*. bechei, but the preopercular sensory canal runs nearer to its deeply concave anterior margin (obviously due to a reduction of the anterior part of the bone) and the tubuli are fewer and relatively shorter. In my opinion the preopercula in the three species, Ph. cf. pusillus, Ph. latiusculus and Ph. bechei, constitute a phylogenetic series which can be derived from the preoperculum in Ph. (?) caffii and from which series the preoperculum in Pholidolepis can also be derived.

In the genera *Pholidophoroides* and *Pholidophoropsis* the preoperculum has a somewhat different shape and the tubules of the preopercular sensory canal are straight and rather short, the longest being situated in the middle part of the bone, not in the ventral half. In all the species hitherto known the shape of the preoperculum is surprisingly uniform. It cannot be derived from *Ph.* (?) *caffii* as directly as can that of *Ph.* cf. *pusillus*, but probably from a still more primitive type. The genus *Pholidophoropsis* cannot, however, be directly derived from *Pholidophoroides*; the members of the latter genus have a relatively high number of infraorbitals, seven against the general number of five; in *Pholidophoropsis* the number of infraorbitals cannot be stated with accuracy, but there is nothing to indicate, at least not in *Ph. maculata*, that it exceeds five.

The structure of the preoperculum thus indicates that within the family Pholidophoridae in the restricted sense given above two diverging lines of evolution may be discerned, the one comprising the genus *Pholidophorus* s. str., probably giving rise to the genus *Pholidolepis*, perhaps leading on to the leptolepids, the other comprising the genera *Pholidophoroides* and *Pholidophoropsis*. In both these lines a reduction of

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the ganoin covering of the exoskeletal cranial bones and body scales has started independently (as probably in many other lines of evolution), in the *Pholidophorus* series from scales with a smooth posterior margin, in the *Pholidophoroides* series from scales with a pectinated or serrated hind margin.

The general phylogenetic evolution can of course be elucidated from other features also, but the material investigated is too fragmentary to illustrate this in great detail. Some indications may perhaps be worth noting.

The sensory pit-lines seem to show a tendency towards a successively more superficial position and consequently their markings on the underlying bones become successively less pronounced. The supramaxillary (horizontal) and postmaxillary



FIG. 16. Diagram illustrating the writer's opinion concerning phyletic relationships between certain genera and species of the family Pholidophoridae s. str., based on the condition of the preoperculum; within the rectangle are species with thin, cycloid scales. The possible derivation of the family from the parasemionotids is indicated by the preoperculum of *Parasemionotus labordei* (Lehman 1952, text-fig. 116). Further explanation in the text.

(vertical) pit-lines on the lateral surface of the preoperculum are rather well marked in *Ph.* (?) caffii and *Ph. latiusculus* (in *Ph.* cf. *pusillus* the lateral surface of the preoperculum is too damaged to enable any accurate statement in this respect), in *Ph. bechei* on the other hand they are very short and easily overlooked. In the *Pholidophoroides-Pholidophoropsis* series these pit-lines are rather well developed in *Ph. limbata*, much shorter in *Ph. maculata*.

The antorbital bone seems to undergo reduction in the holostean-teleostean evolutionary series; in most teleosts it has lost its connection with the infraorbital sensory canal. Unfortunately this bone is unknown in *Ph*. cf. *pusillus*, in *Ph*. *latiusculus* and in *Pholidolepis*; in *Ph*. (?) *caffii* it seems, however, to be relatively better developed than in *Ph*. *bechei*. In the *Pholidophoroides-Pholidophoropsis* series a successive reduction of the antorbital seems to occur; in *Ph*. *limbata* and *Ph*. *crenulata* the antorbital has a rather great postero-dorsal extension and its sensory canal has a relatively long antorbital branch, in the *Pholidophoropsis* species the antorbital is more rounded and the antorbital branch is comparatively short.

My conception of the phylogenetic interrelationship in those members of the family Pholidophoridae s. str. studied by me and based on the shape of the preoperculum and the reduction of the ganoin covering of the cranial bones and scales is tentatively illustrated in Text-fig. 16; the rectangle encloses species with thin cycloid scales.

(c) Some brief comments on the derivation of the family Pholidophoridae s. str.

The question of the ancestry of the Pholidophoroidea has been treated by many authors. Quite recently Gardiner (1960) and Griffith & Patterson (1963) have taken up and discussed the question, also giving a summary of earlier ideas. Gardiner expressly states (p. 350): "From all these facts it appears obvious that the Pholidophoridae have arisen directly from the Parasemionotidae", whereas Griffith & Patterson are somewhat in doubt whether the Pholidophoroidea can be derived directly from that family.

It is not my intention to enter into this discussion; according to Griffith & Patterson the two objections against a derivation of the Pholidophoroidea from the Parasemionotidae (the different course of the facial nerve and of the orbital artery) refer to the endocranium, which I have not studied. I only wish to put forward some remarks regarding certain exoskeletal cranial bones in the family Pholidophoridae s. str.; above all, that our much widened knowledge of the species *Pholidophorus* (?) *caffii* seems to add new facts to this discussion.

As already mentioned above (p. 427) concerning the phylogenetic relationship of the members of the family Pholidophoridae s. str., I consider the preoperculum in Ph. (?) caffii to be the most primitive one, particularly because of the fact that the preopercular sensory canal lies somewhat nearer to the posterior than to the anterior margin of the bone, and that this canal possesses few tubules. In these respects it recalls to some extent the conditions in the Parasemionotidae. In the latter family the preoperculum is at an interesting stage of fragmentation into minor, separate

bones, the variations of which have been clearly demonstrated by Lehman (1052). The antero-dorsal ones of these secondary bones, the so-called "anamestic bones", apparently correspond to the suborbital bone or bones and to the posterior part of infraorbital 3 in more advanced groups (see above, p. 398). The persisting part of the pre-existent palaeoniscoid preoperculum, the preoperculum proper, is pierced by the preopercular sensory canal, which runs near the posterior margin of the bone; generally the canal itself is difficult to observe (at least this was the case in the specimens of Parasemionotus labordei (Priem) which I have had the opportunity to see in Paris and in Stockholm) and an opinion concerning its course can therefore be arrived at only on the basis of the position of its pores. That being so, it is naturally difficult to make out the direction in which the few and apparently very short tubules passed off from the preopercular sensory canal; Lehman (1952, text-fig. 116) depicts them as running in an antero-dorsal direction from the morphologically anterior side of the canal, whereas Gardiner (1960, text-fig. 67D) in his redrawing of Lehman's figure shows them as passing off in a postero-ventral direction from the posterior side of the canal. Which of these two interpretations is the correct one, cannot in my opinion be determined through direct observation, but since the tubules of the preopercular sensory canal, if present, are generally given off from the morphologically posterior side of the canal, the interpretation given by Gardiner seems to me to be the most likely one. If this be the case, the preoperculum in Ph. (?) caffii can easily be derived from that in Parasemionotus (or in some other parasemionotid) through a forward shift of the preopercular sensory canal in connection with a backward lengthening of the tubules given off from its posterior side.

The members of the family Pholidophoridae s. str. generally have two supramaxillaries, whereas the parasemionotids have only a single supramaxillary. In this respect Ph. (?) caffii resembles the parasemionotids, but since this species is represented by only a single specimen, one must keep in mind, as suggested in the description (p. 378), that this may be an individual anomaly. If, in future, further specimens of this species are discovered showing the presence of only a single supramaxillary, Ph. (?) caffii must be removed from the genus *Pholidophorus* s. str. and placed in a genus of its own, a genus which to some extent would be intermediate between the parasemionotids and the family Pholidophoridae s. str.

My opinion that the family Pholidophoridae s. str. (and probably many other pholidophoroids) may be derived from parasemionotid-like ancestors, perhaps still unknown, is demonstrated in Text-fig. 16, in which the preoperculum of *Parasemiono*tus labordei is arbitrarily chosen as representing the parasemionotids.

As compared with Ph. (?) caffii, Parasemionotus labordei is a rather deep-bodied species (Lehman 1952, text-fig. 123). It is therefore perhaps worth noting that in the species *Helmolepis gracilis* Stensiö, obviously belonging to the Parasemionotidae, the size and the shape of the body is about the same as in Ph. (?) caffii. Unfortunately very little is known about the cranial bones of *Helmolepis*, the greater part of the head being missing, which makes a closer comparison between the two species impossible.

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